THE HUMAN SKELETON

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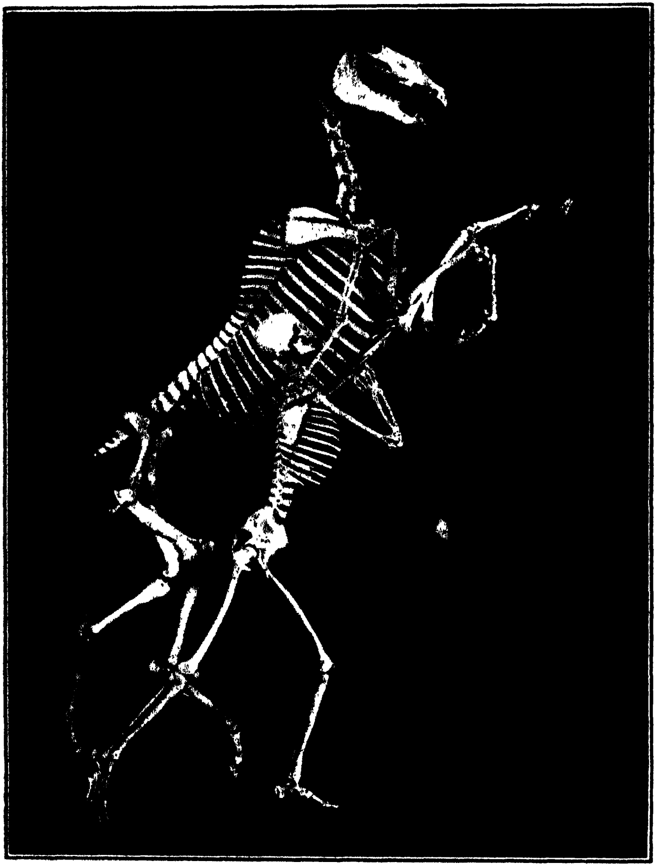
ALEXANDER AND BUCEPHALUS

"Plutarch gives an account of the mode in which Bucephalus came into the hands of Alexander. The horse had been offered for sale to Philip, the prince's father, by a Thessalonian, but had proved so unmanageable that the monarch refused to purchase, and ordered it to be taken away. Alexander thereupon expressing his regret that they were losing so fine a horse for want of skill and spirit to manage it, Philip agreed to pay the price of the steed if his son would ride it. The prince accepted the offer, and succeeded in the attempt. Bucephalus after this, would allow no one but Alexander to mount him, and he accompanied the monarch in all his campaigns." *Anthon's Classical Dictionary.*



MAN AND HORSE

From the group in the American Museum of Natural History of New York City. By permission.

THE HUMAN SKELETON

AN INTERPRETATION

BY

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WITH 175 ILLUSTRATIONS

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TO MY WIFE

ACKNOWLEDGMENTS

The MSS. has been read, destructively and constructively, not only by my wife and various members of my family who could not easily avoid doing so, but also by my assistants in Brown University, Mr. W. Pickles and Mr. J. W. Wilson and by my friendly colleague, Professor A. D. Mead. The many suggestions obtained from all these sources have been gratefully received and for the most part heeded, but since the author prepared the last as well as the first draft, the imperfections of the book as it stands are all his own.

About one-third of the illustrations are original and the most of the others have been redrawn, with due acknowledgment, from various published works.

In the preparation of these sketches, as may be seen wherever initials are appended, assistance has been generously given by two of my pupils, K. L. Burdon and R. S. Stites, as well as by Mr. Wilson and Mr. Pickles. Dr. Walter E. Sullivan of Tufts Medical School furnished the drawing from which Figure 103 was taken, and Mr. Louis R. Sullivan, of the American Museum of Natural History, contributed not only the paragraphs on "Head Deformation in North America" (page 125) but also photographs from which outlines of three abnormal skulls (Figs. 108, 109, 110), were drawn. The Macmillan Company allowed the use of Figure 46, and the *Journal of Heredity* that of Figure 174. Figure 159 is a

hitherto unpublished radiograph obtained through the courtesy of Dr. Peters, superintendent of the Rhode Island Hospital in Providence.

Finally the frontispiece, selected to graphically express the *motif* of the book, is taken by kind permission from the excellent and spirited original group in the American Museum of Natural History, New York City.

To all of these sources I hereby gladly acknowledge my great indebtedness and express my sincere thanks.

H. E. W.

BROWN UNIVERSITY
Jan. 1, 1918.

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A DESCRIPTION AND AN INTERPRETATION

CHAPTER I

INTRODUCTION

1. The Point of View

Every person has a skeleton of his own. To become better acquainted with it is a source of intellectual delight and satisfaction. That is the apology for this book.

The utilitarian reason for understanding more about the human mechanism is, of course, always present. Since the skeleton is an essential part of the bodily machine, which one must use every day as long as he lives, success in living depends fundamentally upon its competent and skilful control.

The wise owner of an automobile is curious to understand for himself the mechanism of his particular machine in order not to depend entirely upon a chauffeur or repair man. An equal amount of curiosity about the individual human organism, which one personifies, is not only pardonable but also almost imperative if in an emergency one is not to resort helplessly to biological chauffeurs and repair men, otherwise known as doctors and surgeons.

Naturally the physician and the surgeon, as well as the trained nurse and the biologist, are expected to take

a professional interest in the human mechanism, since it is a part of their day's work, but too often the ordinary layman seems, subconsciously at least, to regard a consideration of his "insides" as something rather impertinent and indelicate, a subject, in truth, unavoidable whenever complications set in, but quite barren and forbidding to one simply in quest of pleasant or stimulating intellectual adventures.

It is hoped in the following pages to make plain, in some measure at least, that the human skeleton, so often associated unthinkingly with the gruesome symbolism of death, is actually a very wonderful and animated piece of architecture, full of beauty and inspiration for one who looks upon it with a seeing eye and considers its age-long evolution with a comprehending and sympathetic mind.

2. Methods of Study

There are two general avenues of approach in undertaking the study of the human skeleton which may be characterized respectively as the *memory method* and the *interpretative method*.

What is meant by the former method, which was in vogue in the days before the Darwinian Reformation, is well set forth in the introduction to an "Osteology," published in 1866, where the author in explaining why the medical student often delays taking up the presumably dry and difficult study of the skeleton, says, "This is to be accounted for because osteology is difficult of comprehension and often difficult of explanation, for it is rare to find a bone perfect in all its points; and fur-

thermore, it is a subject to be retained by memory alone and not to be assisted by a matter of calculation, as though one character were due to or dependent upon another."

Certainly the study of osteology as thus presented, unassisted either "by calculation" or by a reference of one part to another and made an exercise of "memory alone," would indeed be "difficult of comprehension"! The very fact that it is "rare to find a bone perfect in all its points" makes the structure of which that bone forms a part worth studying. Imperfections in themselves point the way to a reasonable explanation not only of what a bone in question *is* at present but also what it *was* and what it *may become*.

As a matter of fact the human body in every part is a veritable old curiosity shop of imperfections and variations, and, in consequence, it becomes all the more delightful and stimulating to the inquiring mind as an object of study.

In the interpretative method of approach, as contrasted with the memory method, the sister sciences of comparative anatomy, embryology and palæontology all join hands in the eager search for truth, with the result that details formerly unnoted and apparently insignificant take on new meaning and importance, inasmuch as they furnish clues to the riddles to be solved.

CHAPTER II

THE MAKE-UP OF THE SKELETON

1. The Rôle of the Skeleton

The human skeleton is considerably more than a scaffolding for the proper support of the softer parts of the body.

In addition to the function of support there are at least four specific uses to which it is put, namely: (1) giving protection to other parts, (2) furnishing a firm surface for muscle attachment, (3) providing leverage for motion and locomotion, and, (4) with particular reference to the bone-marrow, keeping up the continuous manufacture of blood-cells. These various functions may not all be distinct or mutually exclusive, but they are all accomplished by the skeleton.

2. What is the Skeleton?

The skeleton is the most enduring part of the human machine, that is, it is the last to return to dust after death.

The Greek word *skeletos*, from which the English word *skeleton* is derived, means something "dried up." Ordinarily the idea of a skeleton is associated with dry bones alone, but, although bones form the most conspicuous and lasting part of the skeleton, they by no means constitute the whole of it. When a horse comes pounding

down the street, striking the pavement with an impact of half a ton at every step, it would be shaken all apart if its skeleton consisted only of bones.

Tough connective tissues, ligaments, tendons, sheaths and other structures play an essential rôle, particularly in the supportive function of the skeleton. Parts of the body ordinarily thought to be entirely without a support, as, for example, the liver, the brain or the lymph nodules (Fig. 1), all possess a meshwork of supporting tissue as truly skeletal in character as real bones.

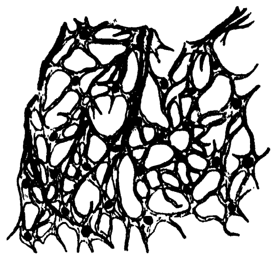


FIG. 1. — Reticular connective tissue from a lymph-gland of a cat to show the supportive skeleton of a soft organ. (After Krause-Schmahl.)

3. Units of Structure

Dating from the pioneer discoveries of Schleiden and Schwann, which were published in 1838–39, it has been generally established that all organic bodies, whether animals or plants, are made up of definite units of structure called *cells*.

These organic building-blocks vary enormously in form and in function but they agree in being microscopically small portions of living protoplasm, usually separated from each other by a somewhat denser envelope or wall and possessing within, a specialized part of living material, known as the *nucleus*, which seems to dominate the activities of the entire cell or unit.

Cells of a kind unite together in orderly array to form

tissues, as, for example, nervous or muscular tissue; tissues in turn combine into *organs*, such as the brain, the stomach or the hand; and finally, organs together make up *systems*, some of which are the digestive, the excretory and the skeletal systems.

In the human frame there are five general types of tissues, namely, epithelial, muscular, vascular, nervous and connective, each of which has a distinct use. *Epithelial* tissues are for the purpose of lining cavities and covering surfaces. *Muscular* tissues, by means of contraction, effect movement. *Vascular* tissues are largely composed of separate blood-cells which, through their ability to circulate, are adapted to carrying on necessary traffic within the body. *Nervous* tissues act as mediators with the external world and also as correlators of all internal activities. *Connective* tissues, comprising the various skeletal parts, while comparatively inactive in themselves, like Aaron holding up the weary hands of praying Moses, make possible the activities of all the other parts.

4. Kinds of Skeletal Tissues

Skeletal tissues in general are distinguished from other tissues by the excessive development of their cell-walls or by the presence of packing material of various kinds between the cells. According to the character of this intercellular substance four kinds of skeletal tissues may be recognized in vertebrates, namely, notochordal and connective tissues, cartilage and bone.

a. Notochordal Elements

In the notochordal tissue, which will be more fully described in the chapter upon the backbone, the intercellular substance is reduced to a minimum. The cells in this embryonic skeletal tissue are comparatively large and thin-walled and are sometimes full of vacuoles (Fig. 2) so that whatever rigidity or stiffness the tissue attains is due principally to a condition of turgor resulting from the fact that its units are crowded into a tough containing sheath, much in the same way that a Bologna sausage acquires a certain degree of turgidity by being made up of many small pieces of meat crowded tightly together within an unyielding tubular casement.

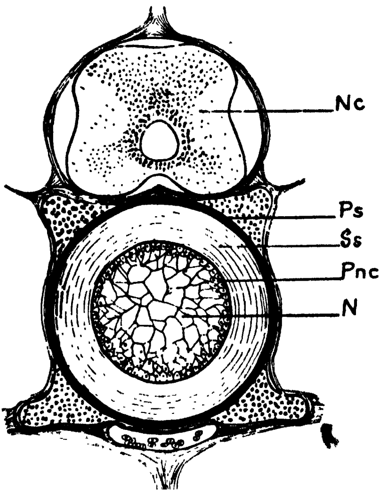


FIG. 2. — Cross-section through the notochord and its sheaths taken from a young dogfish. *Nc*, nerve-cord; *Ps*, primary sheath; *Ss*, secondary sheath; *Pnc*, peripheral notochordal cells; *N*, notochord. (K. L. B.)

b. Connective Tissues

Connective tissues are typically made up of cells in a meshwork of fibrous substance. Among the various kinds of connective tissues one of the best known is

tendon, or sinew, by means of which muscle is attached to bone. Tendons serve a double purpose. In the first place they enable soft, delicate, contractile muscles to gain a firm, tenacious grip upon the solid skeletal parts whereby motion may be effected. In the second place tendons render it possible for the large muscles that make up the most bulky part of the body to be packed in out-of-the-way situations, sometimes indeed at considerable distance from the work to be performed, where they will not interfere by their bulk with the free movement of the joints. The muscles of the calf of the leg, for example, do not enwrap and hamper the ankle joint, although by the aid of slender tendons they bring about ankle movements.

The familiar contour of the human body, which so delights the artistic eye, is very largely determined by the bunching up of muscles that have migrated from the place of their original distribution, a condition familiarly illustrated by the uniform arrangement of the flake-like muscles of a baked fish, into places where they do not interfere with joint action, but still deliver their energy through cord-like tendons to distant points.

The "tendon of Achilles" (Fig. 3), like the electric cable that transmits power generated at Niagara Falls to the industries of distant Buffalo, is a more efficient mechanism for the ankle to have because its muscles are largely concentrated out of the way in the calf of the leg rather than around the ankle itself where they would interfere with freedom of movement.

When tough connective tissues intervene between two bones or cartilages, as, for instance, between the

various bones of the wrist, they are termed *ligaments*. When they connect two muscles they are called *aponeuroses*. Frequently an aponeurosis in the human body marks what previously, in animal ancestry, was muscle tissue. In other words, a skeletal part has replaced a muscular part. A case in point is the aponeurosis connecting the two bellies of the biventer, or digastric, muscle of the lower jaw which in some vertebrates is still a continuous muscle.

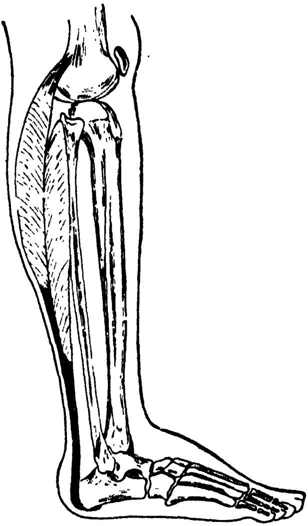


FIG. 3. — The *tendon of Achilles* (in black), showing how the work which muscles do may be applied at a point some distance from the muscle itself. (W. P.)

Connective tissues frequently take the form of tough *sheaths* surrounding more delicate structures, while the sheaths that enwrap muscles become continuous at the ends of the muscle bundles with tendons and aponeuroses.

Again, sheets of connective tissue, termed *fascia* separate one package of muscles from another.

The embryonic notochord, already mentioned and to be considered in detail later, is made up of a tough, tubular sheath stuffed with turgid cells. Moreover, fitting with tailor-made nicety tightly around most of the bony and cartilaginous parts of the skeleton, are tough, vascular sheaths, termed respectively *periosteum*

and *perichondrium.* They form important elements of the skeleton which one is apt to forget when looking at the dry prepared bones of a museum specimen.

Finally, many soft organs of the body have their intricate mesh-like skeletons of connective tissue in the interstices of which lie entangled the proper functional cells, or units, of the organ itself. Thus, the nerve-cells, of the brain or *neurones*, are packed about by supporting skeletal cells, *neuroglia*, which have no nervous function of their own. The secreting cells of the liver are likewise maintained in position by a network of neighborly elements that minister, in a skeletal way, to the true liver cells without in any sense being able to replace them functionally.

c. Cartilage

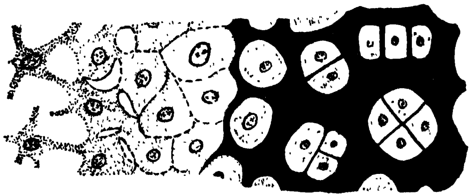
Cartilage is a kind of skeletal substance, practically non-porous, and, except for the perichondrial sheath of connective tissue usually enveloping it, bloodless and nerveless.

Its bulky, yielding character renders it far better adapted for use as a scaffolding for water-dwelling animals, such as fishes, where the denser surrounding medium helps to support the body, than for animals whose weight must be held up in air. Certain fishes, notably sharks and skates, have skeletons wholly or in part cartilaginous in character throughout life. The majority of fishes, however, have a bony rather than a cartilaginous framework. The highest vertebrates, including mankind, not only have a skeleton of cartilage during the early part of life, but also in the adult

condition retain many elements of the same substance left here and there as parts of the hard skeleton.

There may be distinguished at least five kinds of cartilage: primitive, hyaline, ossified, fibrous and elastic.

Primitive cartilage (Fig. 4, B) is a temporary embryonic type that precedes the formation of other kinds but



A B C

FIG. 4. The differentiation of hyaline cartilage. *A*, mesenchyme cells; *B*, primitive cartilage; *C*, hyaline cartilage with the hyaline matrix represented in black, in which the cells are embedded. (After Lewis and Stöhr. J. W. W.).

sometimes occurs in adult structures as, for example, in the fins of certain fishes. In it the cartilage-forming cells begin to secrete a somewhat thicker wall at the expense of the living stuff composing them, with the result that a tissue is formed of ever-increasing stiffness, somewhat as if an orderly pile of pasteboard boxes gradually became boxes of wood.

When this process of cell-wall secretion has gone forward so far that the soft living parts of the depleted cartilage cells are isolated from each other as islands in a surrounding sea of translucent intercellular material, the entire mass is known as *hyaline cartilage*, or gristle (Fig. 4, C). In man hyaline cartilage is found in the bendable, projecting region of the nose; at that end of the

ribs joining the breast bone; in the stiff, incomplete rings that keep the tracheal and bronchial tubes from collapsing; and, finally, in caps on various bones where joints occur.

Whenever the intercellular substance of hyaline car-

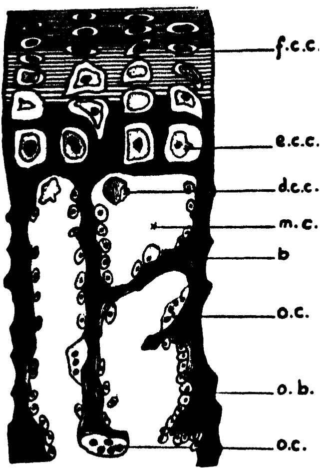


FIG. 5. The formation of bone. *f.c.c.*, flattened cartilage cell; *e.c.c.*, enlarged cartilage cell; *d.c.c.*, degenerating cartilage cell; *m.c.*, marrow cavity; *b*, bone; *o.c.*, osteoclast; *o.b.*, osteoblast. (Modified from Klein. J. W. W.)

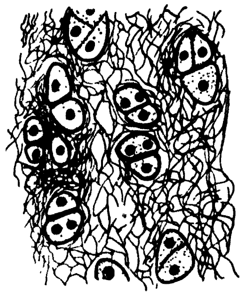


FIG. 6.—Elastic cartilage, from the external ear of man. (After Böhm, Davidoff and Huber.)

tilage becomes infiltrated with limy salts it forms *ossified cartilage* (Fig. 5). This in man usually represents a transition between cartilage and bone.

Fibrous and *elastic cartilage* are alike in having the hyaline intercellular matrix of the cells comprising them interwoven with a tangle of fibers extending in many directions (Fig. 6). These two kinds of cartilage differ

from each other in the character of their fibers. In the former the fibers are white and non-elastic, while in the latter they are yellow and elastic. Fibrous cartilage is typically found in the disc-like pads between the vertebræ, while familar examples of elastic cartilage are presented by the epiglottis or by the framework of the external ear, which fortunately springs readily back into its original shape when bent.

d. Bone

In general, as contrasted with cartilage, bone is porous and supplied with both nerves and blood vessels. It varies considerably in its compactness, being usually spongy on the inside and denser in its outer layers.

Bone consists of two essential substances, first, an organic base of living cells, and second, in the excessively developed walls surrounding these cells, an infiltrated mass of inorganic, limy salts. These two components are so intimately united that there is no visual way of separating them, yet each alone is sufficient to give characteristic shape to a bone; for when the organic part is burned out in fire or the inorganic component is dissolved away by acid, the part remaining in each instance preserves the original form of the bone.

In relative weight the inorganic or mineral part of bone is about three-fourths of the whole, although the ratio of inorganic to organic material varies with age, ordinarily becoming greater the longer the bone lives.

According to Heintz an analysis of the mineral constituents of a human femur resulted as follows:

Calcium carbonate	9.06%
Calcium phosphate	85.62%
Magnesium phosphate	1.75%
Calcium fluoride	3.57%
	100.00%

Embryonically certain active cells, *osteoblasts* (Fig. 5), are responsible for the formation of bone tissue. By their rapid multiplication living bone cells are formed, which in turn secrete the *lamellæ* or hard parts. As bone grows, however, it becomes necessary not only to add new tissue but actually to remove that which has already been formed. For example, when one compares the lower jaw of an infant with that of an adult (Fig. 7) it is evident that no single cell of the former structure can persist unchanged throughout the process of growth. The jaw of the infant is not simply added to as it becomes larger but all of the building material composing it must be broken down bit by bit and reassembled many times before the adult bone is formed. It is as if a stone wall were enlarged not simply by adding to the outside of it as it stands, but by tearing it down and reassembling it in a new place near by so as to enclose a larger area.

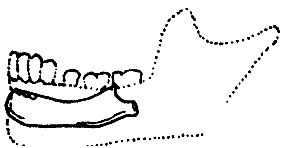


FIG. 7. Diagram comparing the jaw of an infant with that of an adult. (After Kölliker.)

This wrecking of bone tissue which has been once formed, in order to make way for rearrangement and enlargement, is accomplished by certain rather large

definitely identified cells called *osteoclasts* (Fig. 5). The destructive work of these cells is not always followed by constructive reorganization, however, for when the work of the osteoclasts exceeds that of the osteoblasts a bone decreases in size. Thus in toothless old age (Fig. 8) not only the lower jaw becomes smaller through the loss of teeth but also the bony sockets in which the teeth were set decrease in size through removal by the osteoclasts, so that the chin and the nose tend to hobnob together (Fig. 9).

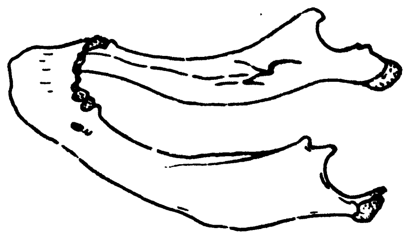


FIG. 8. — The condition of the jaw in old age, showing the acute projection of the chin resulting from the loss of the teeth and the absorption of the sockets for the teeth. (K. S. S.)

Some bones of the body, particularly those of the roof of the skull, are formed by osteoblasts directly, while others, notably those that make up most of the skeleton, are at first formed of cartilage. This temporary cartilaginous scaffolding becomes later invaded by an army of destroying osteoclasts (more properly chrondrioclasts), which are followed up by constructive hosts of osteoblasts, transported to the scene of reorganization from outside the area in question with the result that the cartilage is bit by bit replaced by bone.

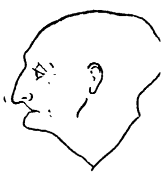


FIG. 9. — "In toothless old age * * * the chin and the nose tend to hobnob together." (After Camper.)

There are large cavities of two sorts within the bones,

one serving the purpose of air-spaces and the other for the storage of marrow. Air-spaces reach their highest evolution in the bones of birds for, as is well known, such bones have become effectively lightened to serve as parts of a flying machine. Air-spaces exist also to a considerable extent in human bones. For example, the *frontal sinuses* in the forehead (Fig. 100) and the *antrum of Highmore* (Fig. 120) in the upper jaw act as air-spaces.

Marrow cavities are present in the vertebrate sternum, ribs and cranial bones, but are particularly evident in the long bones of the appendicular skeleton. The marrow itself may be described as red or yellow. The former kind is the more embryonic in nature and contains an excess of blood-cells, while the latter is yellowish because of the storage in it of a noticeable quantity of fat.

The marrow tissue is the chief factory for the manufacture of red blood-cells. It has been estimated that the life of a single red blood-cell in man is only about ten days. Having been incessantly in motion during this time, while carrying on strenuous chemical commerce throughout the body, such a cell becomes worn out and dies, being replaced by a new blood-cell from the marrow tissue. The total unthinkable number of red blood-cells in a human adult is computed at something like twenty-five billions. To keep up the complement of this mortal host is no small part of the work which the human skeleton has to perform.

When a slice of bone, taken, for instance, from a cross-section through the shaft of the femur and ground down to translucent thinness, is examined under a microscope,

it is seen to be made up of innumerable small plates, or *lamellæ* (Fig. 10). These plates are of hard limy material and are arranged in more or less orderly fashion with reference to the minute spaces which they enclose in

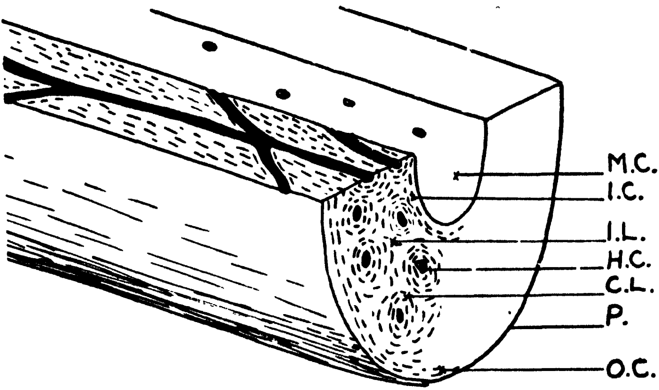


FIG. 10. — A diagrammatic stereogram of bony tissue. Haversian canals and lacunæ in black leaving the bony lamellæ white. *M.C.*, marrow cavity; *I.C.*, inner circumferential lamellæ; *I.L.*, interstitial lamellæ between the Haversian Systems; *H.C.*, Haversian canal; *C.L.*, concentric lamellæ surrounding an Haversian canal; *P*, periosteum, skin-like connective tissue enveloping the whole bone; *O.C.*, outer circumferential lamellæ.

at least three ways, concentrically, interstitially, and circumferentially.

The *concentric lamellæ*, somewhat like the woody rings of growth around the pith of a shrub, envelop small tube-like branching canals, the *Haversian canals*,[1] which permeate the bone lengthwise and are the conduits for the passage throughout the bony tissue of capillaries, lymph-vessels and nerves. The Haversian canals, sur-

[1] Named for Havers, an English anatomist who lived over two hundred years ago.

rounded by their jackets of concentric lamellæ, are most typically seen in the dense tissue of the cylindrical shafts of the long bones in the appendages, where they communicate both through the periosteal coverings of the bone to the outside and also through the entire bony tissue into the marrow cavity within. They constitute the highways for organic traffic throughout the bony tissues, making this part of the skeleton a living adjustable structure.

G. 11.—A diagram showing a fragment of bone tissue at the edge of an *Haversian canal*, through which blood vessels and nerves penetrate the substance of the bone. Eight *lacunæ* each containing a bone cell are indicated and also their connection by *canaliculi*. The bony lamellæ are represented in black.

The necessarily irregular *interstitial lamellæ* fill up the spaces between neighboring Haversian systems, and finally, the *circumferential lamellæ* either surround the entire bone on the outside just beneath the connective tissue sheath (periosteum) that envelops the bone, or as an internal layer they grade over into the spongy tissue that borders the marrow cavity within the bone.

The Haversian canals are not the only spaces, however, that help to make the living bone porous. Between the hard lamellæ separating them from each other are tiny spaces, *lacunæ*, literally "little lakes," in which lie imprisoned the living bone-cells themselves. Lacunal spaces communicate with each other through microscopic holes in the walls of limy lamellæ, called *canaliculi*.

The relation of these structural details is shown in Figure 11.

The distribution of the lamellæ has a direct relation to the mechanical work which bone has to perform. For instance, when a person is standing, the weight of the

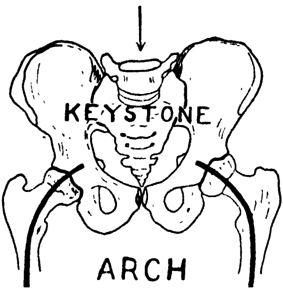


FIG. 12. — A diagram to show how the pelvis forms the keystone of an arch, of which the femurs make up the principal part, for the support of the body.

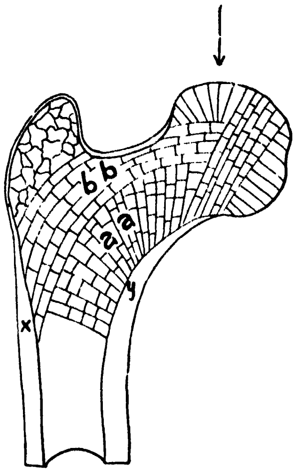


FIG. 13. — A diagrammatic long- [illegible] rough the head of a human fe[illegible]r to show the mechanical arr[illegible]gement of the bony lamellæ for bearing weight. For explanati[illegible] [illegible]e text. (After Jeffries Wyman.)

entire body, with the exception of the legs, comes upon the heads of the femurs. The lamellæ in the femurs are so distributed that together they form an arch extending through the heads of the femurs, with the pelvis for the keystone (Fig. 12). The general way in which spongy bone is arranged at the upper end of the femur so as to

sustain a maximum stress in necessary directions with a minimum of skeletal material, is shown in Figure 13, modified from a diagrammatic drawing by Dr. Jeffries Wyman (1849).

The spongy arch, *bb*, anchored upon the strong dense bone of the shaft at *x*, sustains a pull when pressure, caused by the weight of the body, is exerted in the direction of the arrow, while the buttresses, *aa*, resting solidly against the thicker side of the dense bony cylinder at *y*, like driven piles beneath some superstructure, necessarily resist a compression. Dr. Wyman pointed out that the whole device is much like a bent woody twig where a pull is exerted upon the yielding bark at the convex surface of the bend, while that of the opposite concave side inevitably becomes compressed. In both upper arch and lower buttress the bony elements of the spongy meshwork are effectively arranged with their longer parts massed in the direction of greatest push or pull.

CHAPTER III

NATURE'S EXPERIMENTS WITH SKELETONS

1. The Purpose of this Chapter

The human skeleton of to-day has had a vast and varied number of ancestors.

It presents in each detail the culmination of an endless array of experiments and adaptations that have been going on since the beginning of life on this planet. Moreover, there is every indication that the end is not yet. The skeleton of man is by no means the final mechanism of its kind. There are to be expected in the future other models, based upon all that have gone before and nearer to perfection.

Just as the sociologist in untangling the relationships that constitute modern society must continually enlarge his horizon with respect to existing conditions, and must repeatedly go back with attentive eye to the pages of history in order to find the key to present problems, so the biologist, in attempting to understand and explain the human skeleton, must ever make his vision more inclusive, paying heed particularly to the evidences presented by comparative anatomy.

It is, therefore, the object of this chapter to sketch a background for the human skeleton by considering some of Nature's experiments with skeletons among our poorer relations, the lower animals.

2. The Evolution of the Skeleton as a Protection

a. Protozoa

One of the fundamental functions of skeletal tissues is that of protection for softer parts of the body.

This function is performed, in some degree at least, in the case of nearly every form of animal life. Even among

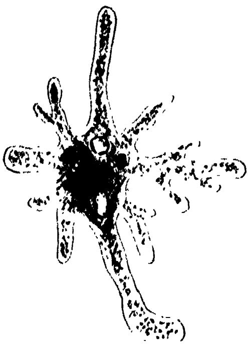


Fig. 14. *Ameba*, a protozoan in which life seems to be reduced to the lowest terms. (After Leidy.)

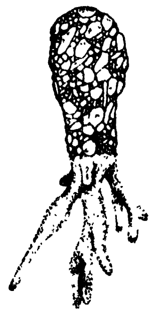


Fig. 15.—*Difflugia pyriformis*, a protozoan with a protective shell of tiny pebbles. (After Leidy.)

the microscopic protozoa, where the entire organism consists of but a single cell, the evolution of a protective skeleton has already made remarkable progress.

When the melancholy Jacques, while discoursing in the Forest of Arden upon the seven ages of man, referred to second childhood as

> "Sans teeth, sans eyes, sans taste, sans everything."[1]

he described quite as well these lowly creatures which,

[1] As You Like It. Act II, Sc. VII.

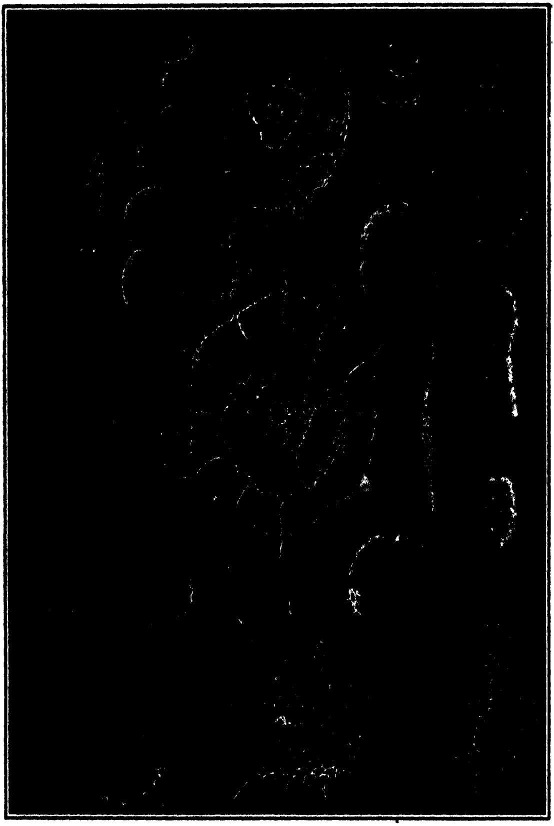


FIG. 17. — Some of the diverse skeletons of *Radiolaria*. (From *Challenger Report*.)

without specific "organs," are still able to perform all the primary functions of life. The *Ameba* (Fig. 14), in which life seems to be reduced to the lowest terms possible, is even "sans" skeleton of any kind.

A related protozoan, *Diffiugia* (Fig. 15), which is much like an Ameba, is housed within a protective gourd-like case made up of tiny foreign particles cemented together except at one end which is open. In *Arcella* (Fig. 16), another member of the same group, the organism secretes a tough chitinous shell from the substance of its own body, and is, therefore, more independent of its environment with respect to the necessary building material for its skeleton. Various other protozoa secrete for themselves protective skeletons of chitinous, calcareous or silicious character, some of which attain a marvellous degree of sculpturing and intricacy of design (Fig. 17). For example, in the *Report of the Challenger Expedition* around the world in the years 1872 to 1876, there are described 4,318 different species of *Radiolaria*, salt-water protozoans with silicious shells, which have lived and died in such prodigious numbers in past ages that their skeletal shells form a considerable part of the sedimentary rocks which make up the earth's crust to-day. Among these little known forms, invisible to the eye when unaided by the microscope, there has been worked out practically every conceivable modification of an outside protective skeleton suitable for the life conditions of such primitive animals.

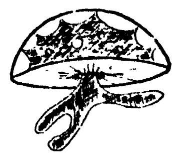


FIG. 16. — *Arcella*, a protozoan which secretes its own chitinous exoskeleton. (After Parker and Haswell.)

But when the plan of the body changes from a single cell to the complexity of many cells, the problem of the protective skeleton becomes correspondingly complex.

b. Worms

In general no hard protective skeleton is found among worms, except in the case of the tubicolous annelids which are provided with skeletal tubes of different kinds. With most worms discretion is the better part of valor and they escape the fate of the unprotected by retreat from danger or concealment from their enemies.

Sometimes, however, as in the case of the "vinegar eels," microscopic worms frequently found in vinegar, a dense, impervious cuticle protects the animal from its acid environment which, were it not for this, would be ruinous to the soft parts of the body.

c. Echinoderms

Echinoderms, of which the familiar sea-urchins and starfishes are examples, are furnished with a different device for a protective skeleton consisting of many calcareous plates regularly distributed and embedded in the skin (Fig. 18). Each plate is enlarged by marginal growth so that the animal within is accommodated as its size increases. These plates are frequently rendered more efficient by bearing fixed or movable spines on their outside surfaces, thus presenting a formidable defence against hostile attack.

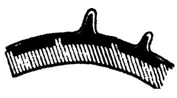


FIG. 18 — Limy plates (in black), embedded in the skin of a starfish.

d. Crustaceans

It is among the crustaceans, however, of which the lobster (Fig. 19) is a conspicuous representative, that the

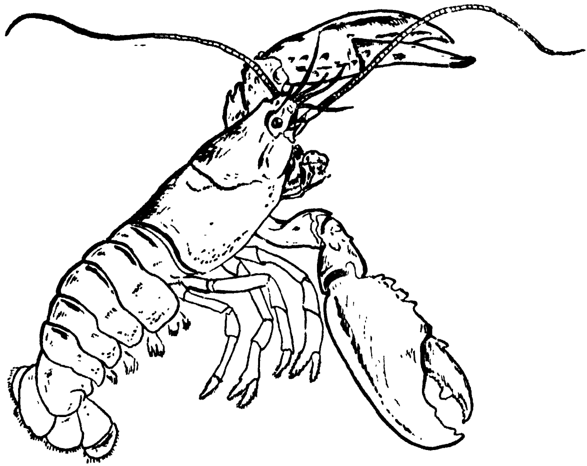


FIG. 19. — The lobster, an exponent of the exoskeleton idea.

idea of an external protective skeleton reaches its greatest elaboration.

The *hypodermis*, or single-layered skin of these animals, secretes all over the exterior of the body a chitinous deposit of varying thickness which may sometimes be strengthened in places by an additional impregnation of limy salts. This chitinous covering extends to all the appendages and includes even the minutest "hairs" that appear in various parts. Flexibility is made possible in this continuous envelope of chitin by thin accordeon-like folds at the joints, while tactile sensation is at-

tained principally by means of projecting antennæ, likewise gloved over with the chitinous exoskeleton.

This hard, non-cellular, protective crust of the crustaceans is a lifeless armor which does not change its size after it has once been secreted. The animal within, however, like all living things, grows larger, and fitting more and more tightly in its case, it is eventually forced to burst open the dead, unyielding envelope that encloses it. This is the process of molting.

In the case of the lobster the skeleton splits open down the back and the animal gradually humps its soft body out of the crack, withdrawing one by one all of its several appendages, not, however, without frequent damage to them. As soon as the perilous operation of molting is accomplished, the lobster, before beginning to secrete a new shell, improves the opportunity thus afforded to swell up to considerably more than its former size by an excessive intake of water.

Thus among the crustaceans a protective exoskeleton is maintained but not without much exposure to injury and repeated physiological expense in the loss of the shell which such animals go to the trouble of elaborating.

c. *Insects*

In the great class of insects, which includes over twice as many kinds of animals as all other groups together, the exoskeletal plan has been continued, although it has undergone considerable modification for the purpose of life in air instead of in water. This change has been accomplished in two ways, first by the secretion of a

thinner exoskeleton, and second by a restriction of the process of molting.

The covering of insects is much lighter and more delicate than that of their crustacean cousins, although it is similarly everywhere present like a thin, impermeable varnish spread entirely over every exposed part. Moreover, by the evolution of *metamorphosis*, a process whereby growth for the whole period of the life cycle, with accompanying molting, is accomplished entirely during the larval stage, the difficulty of periodical molting throughout life with its attendant disadvantages has been in part avoided, thereby leaving the insect free from this handicap during maturity. It is a state of affairs much like that among people of acquiring lifelong immunity from certain contagious diseases by contracting them during infancy when time is less valuable and the general inconvenience is not so great as in later life.

One reason why the insect plan has proven itself numerically to be so successful is perhaps because the protective exoskeletal shellac peculiar to this class of animals extends as a lining some distance into the digestive tube, thereby forming an effective barrier against bacterial invasion. Probably the majority of animals, aside from insects, succumb, directly or indirectly, to bacteria, a fate rare in the case of insects.

From the evolutionary point of view, however, there is a paramount objection to a protective exoskeleton since the increasing burden of an enlarged armor soon becomes insupportable, necessitating a limit in the size of the body encased within it. The imagination hesitates to picture a beetle as bulky as a cow, for the largest known member

of the enormous group of insects is probably smaller even than the smallest adult bird or mammal.

f. Molluscs

There remains to be considered one other way in which the problem of an exoskeletal protection has been solved in the animal kingdom, namely, the method typified in the group of molluscs.

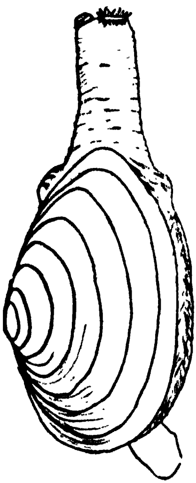


FIG. 20. – A clam shell showing lines of growth. (After Morse.)

The soft bodies of molluscs are generally protected with limy shells secreted by a special enveloping organ called the *mantle*. These exoskeletal shells are an effective protection against ordinary enemies and, when once they have been secreted, are never wastefully molted after the crustacean fashion. The parsimonious molluscs keep every particle of their old shells, simply adding new layers on the inside as growth demands. The layers, being a little more extensive at each addition, form by their edges so-called "lines of growth" showing as ridges on the outside of the shell (Fig. 20).

This experiment in skeletons, however, has cost the group of molluscs dear, for the heavy shell, together with the policy of passive defence made necessary by it, has either impeded the power of locomotion, with all at-

tendant advantages for the evolution of sense-organs and a central nervous system, or compelled its complete abandonment. The clams and their allies, therefore, have lagged behind in the race for life, or stuck conservatively in the mud, while other animals, without such an incubus as the molluscan shell, have toiled successfully on to higher levels in working out their organic salvation.

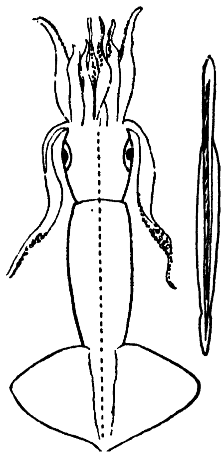


FIG. 21. — Outline of a squid with the skeletal "pen" at the right. The dotted line shows where the pen is embedded in the body. (After Lucas.)

One group of molluscs, the *cephalopods*, of which the squids along the Atlantic coast are familiar examples, has finally succeeded in throwing off a dead, protective exoskeleton, by which like an "Old Man of the Sea" their ancestors were so long borne down, and this group, in consequence, has approached the higher estate of the vertebrates whose skeleton has become a living, internal structure. The cephalopods have not only discarded an external skeleton, although still retaining the mantle to secrete one, but they have evolved at least a hint of an internal skeleton in the form of a stiff "pen" or "cuttlebone," a structure which, although secreted and dead, lies embedded within the body-wall as a prophecy of better things (Fig. 21).

g. Vertebrates

The *endoskeleton* of the vertebrates, which is primarily a device for the function of support, is, in addition, largely a protective apparatus. For instance, the brain-case and the spinal column protectively enclose the central nervous system, while the thoracic basket, which is made up of vertebræ, ribs and sternum, provides effective sanctuary for various important soft organs.

In general, however, the protective uses of the skeleton have given way, during the long course of evolutionary development, to the increasing importance of the skeleton as a support or scaffolding for other parts. Figure 22 indicates diagrammatically the way in which the function of protection gives way to that of support as one goes up the evolutionary series.

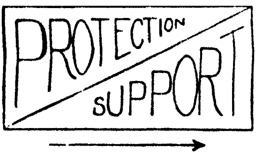


FIG. 22.—Diagram to show the reciprocal relation of the functions of protection and support in the skeleton. The trend of evolution is in the direction of the arrow.

Finally, even among the vertebrates, dominated and typified as they are by their successful endoskeletons, exoskeletal relics of past evolutionary days may still be found to which reference will be made in a later chapter.

3. THE EVOLUTION OF THE SKELETON AS SCAFFOLDING

The shifting of the chief skeletal function from protection to support has in a measure made possible a gradual increase in bulk among the representatives of the evolutionary series from the protozoa to the vertebrates.

The supportive function has become all the more

necessary since, in the transformation of species, forms of life have emerged upon the land from the ancestral nursery in oceanic waters. An aquatic form like a jellyfish, buoyed up by the surrounding medium in which it lives, is by no means in such dire need of a supporting framework as an animal out of water in air would be. A jellyfish cast up on the beach, however, without a skeletal support suitable for land conditions, is quite helpless. So necessary, indeed, is a supportive skeleton for life on land that only a few animals could be cited which are thus unprovided.

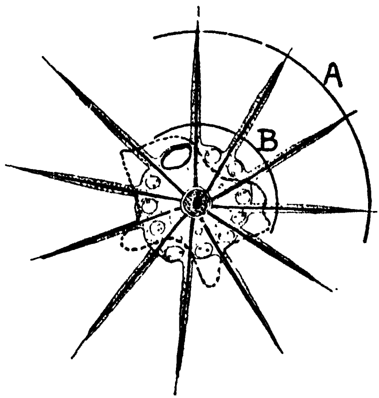


FIG. 23. A diagram of a *heliozoan* which is able by its supportive skeleton to explore without locomotion an environment as large as the circle *A*. The dotted line represents an *Ameba*, which although of equal bulk is able to extend itself only as far as circle *B* without locomotion.

a. Heliozoa

In stagnant water there is sometimes found a microscopic protozoan, *Actinophrys sol* (Fig. 23, A), first described by Ehrenberg in 1830, whose fragile anatomy is characterized by numerous secreted rods, or axial filaments, to the sides of which adheres a film of streaming protoplasm continuous with the body of the cell itself. These rods stick out in every direction, resembling the rays of the sun, hence the group to which this organism belongs is called *Heliozoa*, or sun animals.

The advantage of the device is obvious. By utilizing a scaffolding of this kind, the tiny bit of protoplasm that forms one of these animals can without the necessity of locomotion, be made to spread out and explore a much larger neighborhood in search of food particles than it would be possible for an Ameba to reach with the same bulk of living material but without such a mechanical aid. This is diagrammatically shown in Fig. 23.

b. Sponges

Sponges are primitive animals some of whose component cells are so mob-like in arrangement and so poorly adapted for working in unison that they can scarcely be regarded as having attained to the degree of organization characteristic of true tissues. They represent about the first attempt of organic units to live together in harmony as an organism. With the partial loss of their independence these cells exhibit the beginning of a commendable division of labor among themselves, a first step, one may say, in efficiency.

FIG. 24.—Types of isolated spicules, making up the skeletons of sponges.

For example, some sponge cells are *flagellate*, and by lashing the water serve to bring food particles to the colony; some are *ameboid*, engulfing the food that is brought in; some are *germinal*, providing for the main-

tenance of the species; and finally, some are purely *skeletal*, holding open necessary passageways for the other cells to do their work. The skeletal elements (spicules) are secreted by the spicule cells, and may be composed of limy, glassy or, in case of the common bath sponge, fibrous material. They assume a wide range of forms, as for example, rods, boomerangs, tripods, stars and anchors (Fig. 24) all tumbled together like so many jackstraws. Usually they are not attached to each other although they sometimes interlock and, in the case of the fibrous sponges, entangle together in a continuous meshwork. They represent the simplest sort of a skeletal scaffolding to be found among many-celled animals.

FIG. 25. — A hydroid colony consisting of colonial flower-like animals with a transparent exoskeleton. See Fig. 26. (K. L. B.)

c. Celenterates

In the great, diverse salt-water fraternity of the celenterates, to which the hydroids, jellyfishes, sea-anemones and corals belong, many notable experiments in supportive skeletons have been worked out.

The hydroids, for example, are delicate little flower-like animals that may be regarded as animated mouths favorably situated at the ends of branching twigs (Fig. 25). These mouths are surrounded by a crown of active tentacles and open, in each instance, into a capacious digestive sac below. The reason they are found arranged together like the twigs of a tree is that they bud

out, plant fashion, one from another. This results in a radiate disposition of individuals which is the best possible way for a colony of attached animals to be arranged in order to reach the greatest possible environment in the search for food.

FIG. 26. — Two hydroid individuals enlarged, showing *perisarc*. (K. L. B.)

To maintain these fragile creatures in attitudes of greatest efficiency a mechanical support is necessary. Such a support is provided by the *perisarc*, (Fig. 26), a thin but stiff sheath of secreted material loosely enclosing each stem which, in the case of the campanularian hydroids, forms a terminal, transparent protective bell into which the contractile organism can retreat upon occasion.

In the closely related corals the sheath corresponding to the perisarc is heavily impregnated with limy salts (Fig. 27), and the stony twigs thus formed become fused together with ever increasing ramifications due to the continuous budding of the formative coral animals within. Individual coral animals die in myriads leaving their scaffolding behind as a foundation upon which their innumerable offspring may in turn rear calcareous prisons until finally, from the accumulation of the remains of these supportive skeletons, vast land-forming masses rise from the ocean level.

FIG. 27. — A piece of a coral colony with an exoskeleton of lime.

d. Vertebrates

All the foregoing skeletons, however, are external and lifeless.

It has remained for the vertebrates to become the exponents of a higher and better plan, namely, of an *internal living skeleton*, on the outside of which the other organs of the body are supported. This is not simply an improvement over preceding devices. It is a brand-new idea of far-reaching evolutionary significance. An internal skeleton is a changeable living structure, which through its continuous adaptability keeps pace with the increasing demands of the enlarging organism.

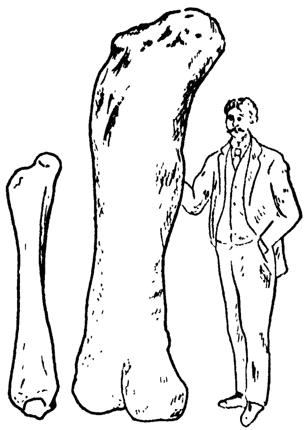


FIG. 28.—Thigh-bone of a dinosaur, *Camarasaurus*, in the Field Columbian Museum. This is the largest known bone. On the left for comparison is the thigh-bone of the largest known elephant. (After Lucas.)

With the introduction of such a scheme of mechanical support the ban upon size, imposed by the lifeless exoskeleton, was lifted and the golden age of gigantic monsters dawned. Throughout Mesozoic times Nature revelled in the possibilities of this new skeletal plan. Some of the enormous creatures which lived in those days, ***dinosaurs*** (Fig. 28), ***plesiosaurs***, ***theromorphs*** and other monsters, lifted tons of flesh into the air upon majestic bony scaffoldings. These proved impractically

large, however, and, after recording the results of the experiment by means of their fossil remains, they vanished forever from the face of the earth.

There still remain elephants on land and whales in water as living illustrations of how far it is possible to go in the matter of size when an adequate internal support is provided.

4. Evolution of Skeletal Surface for Muscle Attachment

In order for muscles through their contraction to be effective in producing motion or locomotion, it is necessary in most cases for them to secure adequate skeletal attachment. The intrinsic muscles of the tongue are a notable exception. It follows, therefore, that an important feature of any skeleton must be sufficient surface conveniently placed to give foothold to the muscles.

It is true that there are various involuntary muscles, such as those in the walls of the intestine responsible for peristaltic movements, as well as a few voluntary muscles like the sphincter muscle that closes the anus or the whistling muscles of the lips, which are not directly attached to hard skeletal parts; but most muscles are so connected both at their origin and at their insertion.

One reason why exoskeletal animals, such as insects, crustaceans and molluscs, are limited in size, is the fact that in their case the muscles must be attached on the inner surface of the shell consequently, the exoskeleton must always be larger than the muscles. In a lobster (Fig. 19), for example, muscles large enough to operate effectively a pincer-like claw require for their attachment

such a sizeable exoskeletal covering that clumsiness and inefficiency are unavoidable results.

Among the vertebrates flying birds present the extreme evolution of relative skeletal surface. In these aërial machines the powerful muscles of flight not only demand an expansive widened sternum but there also has been evolved upon this sternum an additional plate of bone called the keel, which is placed at right angles to the original sternal bone, thus doubling its available surface without adding disastrously to the total weight (Fig. 29). Moreover, in birds the ribs are peculiarly flattened, so that the same material is made to present an increased surface for muscle attachment. The ends of the femurs also, as well as the ends of the other long bones of the leg and foot, have a larger surface than the corresponding mammalian bones.

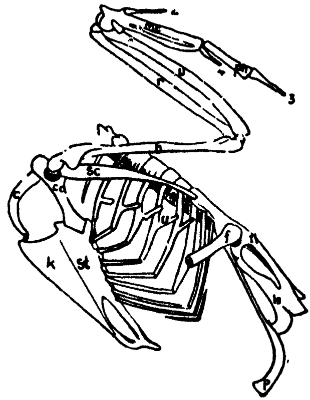


FIG. 29. A part of the skeleton of a goose, showing breast-bone with keel (*k*). (After Kingsley.)

Large animals have relatively greater areas for muscle attachment than small animals, as that famous observer, Galileo (1564–1642), pointed out long ago. Figures 30 and 31 show reduced to the same scale, the skeletons of two mammals that actually vary greatly in size. A glance will show that the bones of the enormous hippopotamus present considerably more external sur-

face *relatively* than do those of the tiny lemming. Thus it is inevitable that the larger animal does relatively

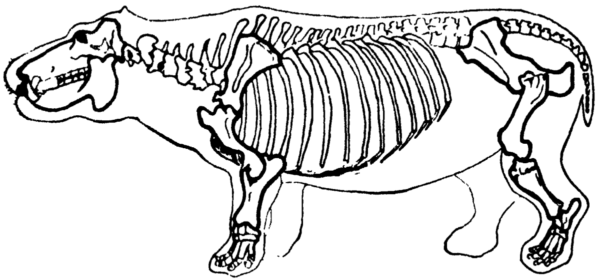


FIG. 30. Skeleton of a hippopotamus, reduced to the same scale as the skeleton of the lemming shown in Fig. 31. (After Hesse.)

more muscle work than the smaller one. This is because bulk, which is measured by three dimensions, increases faster than surface, which is a matter of two dimensions.

In the case of man conspicuous skeletal surfaces are

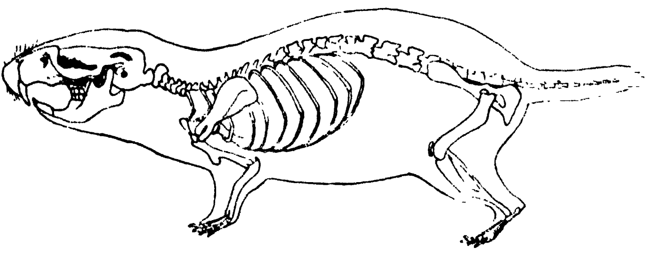


FIG. 31. – Skeleton of a lemming. (After Hesse.)

exhibited by the innominate bones of the pelvic girdle to which are attached muscles concerned with the upright posture (see frontispiece). The broad shoulder-blades, too, furnish anchorage for muscles that operate the arms which, upon man's attainment to the upright posture,

became emancipated from locomotion and were turned to new and diverse uses.

5. The Evolution of Skeletal Levers for Locomotion

The power of locomotion is vastly more important for animals than for plants.

It is well known that most terrestrial plants are stationary while the majority of animals are characterized by some method of locomotion. This difference depends largely upon food.

The chemical elements that go to make up living matter, and which must be furnished by food, are essentially the same for both animals and plants. These elements are of very nearly universal distribution in air and soil in the form of water, carbon dioxide and inorganic salts (see Fig. 135, Chapter X).

An ordinary plant by means of green coloring matter, *chlorophyll*, is able in the presence of sunlight to combine these inorganic substances into organic compounds which serve as its food. It does not need the power of locomotion to find these things and consequently is usually stationary.

An animal, on the contrary, unlike a plant, is not able to build up its food out of inorganic supplies and must, therefore, make use of material that plants have primarily made available. Such organic material is not as widely distributed as the inorganic resources upon which plants draw, so that when an animal uses up the food within reach it must locomote for more. The necessity of

locomotion for food has thus in the case of animals created a very definite problem for evolution to solve. The way it has been worked out is of great interest.

a. Protozoa

Two general methods have been tried and found adequate by the microscopic protozoa.

First, the whole plastic body of the cell may flow out in any direction, withdrawing at the same time from other regions. This is *ameboid* locomotion and the parts of the cell which accomplish it, *pseudopodia*, are always temporary makeshifts, constantly renewed as occasion demands (Fig. 14).

The second type of protozoan locomotion is *ciliary*. By means of this method relatively permanent hair-like projections of protoplasm, *cilia*, either few or numerous, lash the water like oars and so send the animal forward (Fig. 32). Ciliary locomotion serves very well for tiny organisms in a relatively dense medium like water, but with increase in the size of the organism this method proves inadequate. The ciliary device may be compared to the triremes of the ancient Romans which were propelled by rows of oars. Obviously it would be quite impossible for a modern battleship or ocean liner to carry a sufficient number of galley slaves to row such a vessel about by the oar method.

FIG. 32. *Stylonychia*, a protozoan that locomotes by means of cilia. (After Delage et Hérouard.)

b. Flatworms

The use of cilia for locomotion in animals of considerable size is shown in ordinary freshwater flatworms, *planarians*, which are familiar to those people whose curiosity impels them to look on the under side of stones and sticks in small streams and around the edges of ponds (Fig. 33).

These interesting animals, which are frequently as

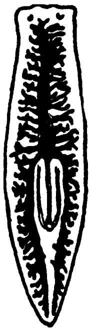


FIG. 33. — A flatworm, an animal without a hard skeleton.

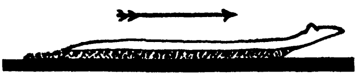


FIG. 34. — Diagram of a flatworm from the side, showing how a track of mucous is secreted in which cilia make effective strokes for locomotion. (After Pearl.)

much as an inch in length, glide along by means of innumerable cilia the strokes of which are made effective because the worm secretes a mucous track as it moves. In this medium, which is denser than water, the cilia encounter enough resistance to propel the animal forward (Fig. 34). Such a method of locomotion without skeletal aid is both laborious and slow.

c. Locomotion in Water and on Land Contrasted

Various locomotor devices in which some kind of a skeleton takes part have been evolved among animals that inhabit water. The problem of locomotion becomes something quite different, however, as soon as animals emerge upon land. The difference of density between water and air is so great that a mechanism which is successful in water would prove entirely ineffective when operated in the thin and comparatively non-resistant medium of air. The flat tail of a fish, for example, by lateral strokes in the dense medium of water sculls the animal forward, just as, similarly, the muscular abdomen of a lobster by sudden snapping shoots the submerged animal backward; but neither of these mechanisms works on land.

In the case of land animals friction is increased because they must rest upon a substratum, while fishes, on the other hand, are usually buoyed up in water and so do not ordinarily come in contact with the bottom.

d. Locomotor Levers upon Land

One of the first stages in the evolution of locomotion upon land has been the elevation of the elongated body off the ground on to stilt-like legs so that the amount of friction surface is minimized and at the same time a system of skeletal levers is developed upon which the muscles of locomotion may act in propelling the animal forward.

So long as the body is not elevated off the ground, as, for example in myriapods and caterpillars, the number of legs is not necessarily limited, but there seems to be some

advantage in the direction of specialization in reducing the number of duplicated organs as soon as possible. Spiders walk upon eight legs and adult insects upon six while vertebrates never possess more than four legs, a number which reduces to lowest terms the props that may logically support an elongated bilateral body. The small boy who wrote in his composition that the cow had "four legs, one under each corner" was architecturally correct.

The next stage in specialization is tipping the body up on end and balancing it upon two legs.

With the birds this resulted in the emancipation from ground locomotion of the fore legs, which then evolved into wings whereby a new realm, the upper air, has been conquered for animal locomotion.

In primates, as typified by man, the upright posture with the resultant bipedal method of locomotion wrought evolutionary consequences of the most far-reaching importance. The way was then opened for the human hand, destined to hold a tool and to harness the forces of Nature, and furthermore, the weight of the evolving brain within its cranial citadel was shifted from a mechanically awkward position, like the figure-head of a ship held out by main strength at right angles to the main axis, to a position of perfect poise crowning the top of the upright vertebral column, where it is maintained at slight mechanical expense.

6. Conclusion

The conclusion that must be drawn from this wandering excursion into the comparative anatomy of skeletal

structures, is that the human framework represents a battle-scarred makeshift in which the various functions of support, protection, muscle surface and leverage have all left their mark, and in which no detail of structure is to be found that does not owe its characteristics to a long ancestral line of evolutionary adaptations.

CHAPTER IV

EXTERNAL SKELETAL TRIMMINGS

1. The Vertebrate Skin

It has been shown in the preceding chapter that the typical protective skeleton is external and lifeless, entailing the necessity of periodical molting, while the functions of support and leverage are best performed by an internal living skeleton.

The invertebrate skin, or *hypodermis* (Fig. 35), which by secretion forms the exoskeleton, is made up of a single layer of cells, while the skin of vertebrates is double in character, being composed of an outer *epidermis* and an underlying *derma* (Fig. 36).

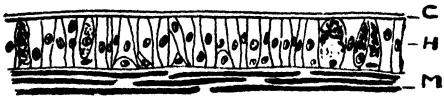


Fig. 35. — A section through the skin of an earthworm. *C*, cuticle secreted by the hypodermal cells; *H*, hypodermis; *M*, muscles. (After Schneider.)

Since capillaries and nerve-endings do not penetrate into the outermost or corneal layer of the epidermis, this region of the vertebrate skin is quite without sensation, suggesting the dead exoskeleton of the crustacea.

The way in which the outer lifeless layer of the vertebrate epidermis is formed may be shown by describing what happens in the human skin. The human epidermis originates from a layer of active germinative cells known as the *Malpighian layer*,[1] which lies next to the denser

[1] Named for Marcello Malpighi (1628–1694.)

interwoven derma. As the cells of the Malpighian layer multiply vigorously, some of their progeny are pushed out toward the surface, becoming more and more flattened and together forming a tissue of many cells in

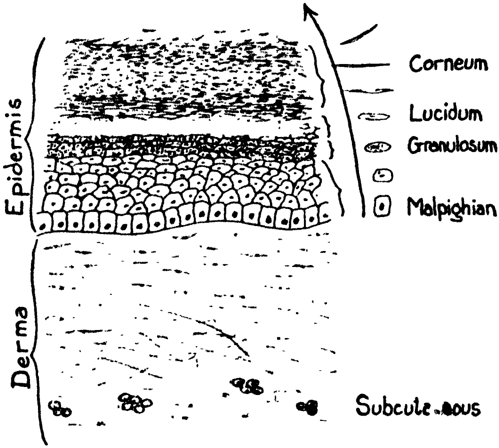


FIG. 36.—Diagram of the skin showing how the Malpighian layer gives rise to the superimposed layers of the epidermis.

thickness. The oldest and outermost cells, which constitute the so-called *corneal layer*, become quite lifeless, however, by gradually losing their protoplasmic contents, so that practically nothing but the flattened cell-walls remain. In this condition each of these cells may be compared to the skin of a grape from which the pulp has been squeezed out.

The remains of these dead cells are continually being loosened and cast off from the surface of the skin, as, for instance, the dandruff of the scalp, but they are just as

constantly being replaced from the living Malpighian layer below.

A condition parallel to the molting of invertebrate exoskeletons thus occurs among vertebrates, varying in degree with different types of animals. Among salamanders and frogs the dead outer elements of the epidermis hang together like a gauzy covering which comes off almost entire, while among toads it is shed in shreds and tatters. The way in which a snake "sheds its skin" is well known. Not the whole skin nor even the whole epidermis is lost but only the dead corneal layer is loosened and cast off, while a new protective corneum is forming underneath.

The feathers of birds are conspicuous protective skeletal structures which are a direct product of the Malpighian cells of the epidermis. Feathers are repeatedly undergoing the process of molting and replacement as are likewise the hairs of similar epidermal origin that characterize mammals.

It is the purpose of this chapter to consider briefly these dead epidermal reminders of invertebrate protective skeletons which are still to be found among the vertebrates generally, even in man.

2. Scales and Teeth

a. Placoid Scales

Among the exoskeletal relics surviving in vertebrates are teeth which are homologous to, that is, formed in the same way as, the scales of certain fishes, notably the *selachians* of which the sharks, skates and dogfishes are representatives. These fishes are clothed with tiny

placoid scales, which resemble thumb-tacks closely embedded side by side with their points projecting out-

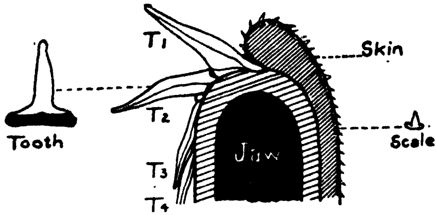


FIG. 37. — Diagram of the edge of a shark's jaw to show the relation of placoid scales and teeth. *T1*, tooth in service at edge of jaw; *T2*, *T3*, *T4*, reserve teeth. (K. L. B.)

ward and backward. At the edges of the jaws, where the skin passes over continuously as the lining of the

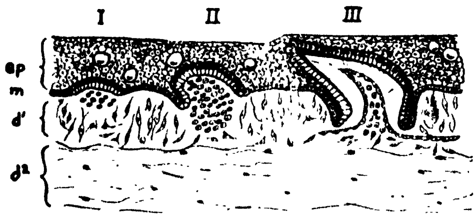


FIG. 38. A section through the skin of a fish to show the formation of placoid scales. *ep*, epidermis; *m*, Malpighian layer from which the epidermal cells originate; d^1, loose dermal tissue; d^2, stratified dermal tissue. Stage I, the Malpighian layer beginning to bulge up and dermal cells collecting under the cap. Stage II, continuation of the process. Stage III, formation of the enamel tip of the scale (in black) under the Malpighian layer and the elaboration of the dentine part of the scale by the osteoblast-cells of the derma. (After Schimkewitsch.)

mouth, they are transformed into teeth, which, in the selachians, are arranged in successive ranks one behind another just within the margin of the jaws (Fig. 37).

The fact that teeth are simply modified placoid scales becomes more apparent when a comparison is made of the development of the two kinds of structures.

In the skin of an embryo shark, for example, wherever a placoid scale is about to form, the Malpighian cells of the epidermis increase in number so rapidly that they bulge up into a tiny cap, the *enamel cap*, which pushes out eventually and projects through the skin (Fig. 38). Just below and within this hollow enamel cap are crowded cells from the underlying derma that are destined to form the *dentine*, or ivory, that makes up the bulk of the hard scale. These two components, the enamel and the dentine, then fuse together into the individual scale, now embedded in the skin which gave it origin. Thus a part at least of the placoid scale is of epidermal, or exoskeletal, derivation.

b. Development of Teeth

Similarly in the case of a human embryo, the Malpighian cells of the epidermis, beginning about the seventh fetal week, start into accelerated activity along the edges of the jaw where the future teeth are to be and invade the underlying dermal tissue in the form of the so-called *dental ridge*. All along this dental ridge, wherever a tooth is later to appear, the rapidly increasing Malpighian cells shape up into cone-like caps pointing outward (Fig. 39). These are the enamel-caps that finally may become quite isolated from the layer which gave rise to them. Under such an enamel-cap crowd the surrounding dermal cells that are to form the dentine of a tooth until the whole compound structure intimately

fuses together quite after the fashion of a placoid scale. All that now remains is for the enamel-capped ivory

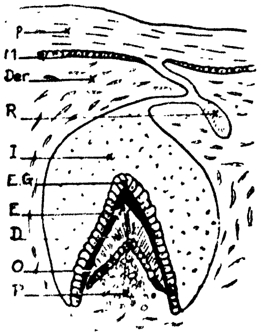


FIG. 39. — Diagram to illustrate the development of a tooth. *Ep*, epidermis; *M*, Malpighian layer of epidermis; *Der*, derma; *R*, reserve germ; *I*, remains of intermediate cells; *E.G.*, enamel germ cells from Malpighian layer of epidermis; *E*, enamel (in black); *D*, dentine; *O*, odontoblasts forming the dentine; *P*, papilla-cells from derma.

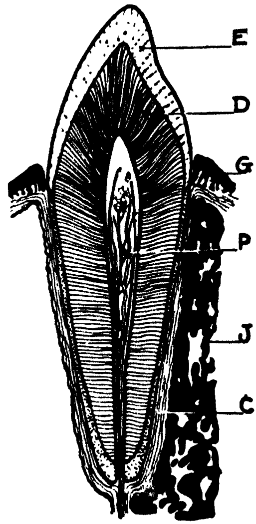


FIG. 40. — Diagrammatic long section through a typical canine tooth. *E*, enamel; *D*, dentine; *G*, gums; *P*, pulp cavity in which are capillaries and nerve-endings; *J*, jawbone; *C*, cement. (K. L. B.)

contrivance thus initiated to erupt slowly through the gums by the irresistible powers of growth, and "the baby has cut a tooth!"

c. A Typical Tooth

The general structural details of a typical tooth are shown in Figure 40.

The *crown* is that part which projects beyond the

gums; the *roots* are embedded in the sockets of the jaw; and the *neck* is in the region covered by the gums between the two first-named parts. The tooth itself has a cavity within it, called the *pulp-cavity*, which is invaded by blood-vessels and nerves that gain entrance through the opening at its base. Neither blood-vessels nor nerves, however, penetrate the substance of the tooth itself.

The solid part of the tooth is of threefold character. The larger part of it is *dentine* or ivory, a tissue denser than bone but, nevertheless, permeated with tiny radiating canals. Outside the dentine around the roots is what

FIG. 41 — Jaws of a garpike, showing primitive grasping teeth.

is known as the *cement*, a bonelike substance that fixes the tooth in its socket. Over the crown, where exposure to wear comes, the dentine is protected by a layer of *enamel*, the hardest, densest, most enduring tissue of the human body.

d. Differentiation

The teeth of primitive water-dwelling vertebrates are commonly alike in form, usually more or less pointed, and thus adapted to serve as hold-fast organs to enable these handless animals to grasp their food (Fig. 41).

Ordinarily the lower animals gulp their food whole. The refinement of chewing appears later in evolutionary history. When the occasion for chewing arose, the teeth,

particularly the back teeth near the angles of the jaws where the leverage is greatest, became modified into flat-topped *molars* which assumed the function of crushing and chewing. Meanwhile the front teeth, notably in the case of rodents, became specialized into cutting

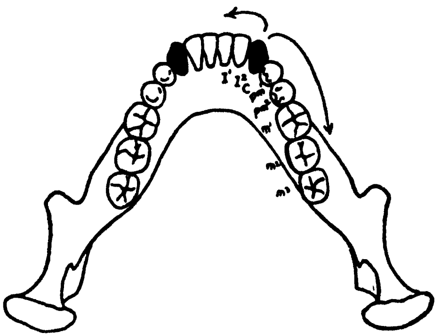


FIG. 42. — A human lower jaw, showing (by arrows) the two general types of tooth differentiation from the primitive pointed canine tooth (in black).

chisels, *incisors*, to divide the food into morsels of convenient size for the grinding mill of the molars.

Figure 42 represents a diagram of adult human dentition in which the dual character of differentiation from the primitive type is quite apparent.

The most ancestral and least changed of all the teeth are the cone-shaped *canines*, or "eye teeth," which are quite like the pointed, grasping teeth of the lower forms. On either side of the canines modification has taken place progressively in divergent fashion, as indicated by the arrows, on the one hand toward the more chisel-like type of the incisors and on the other toward that of the flat-topped molars.

e. Succession

The placoid teeth of the selachians are present in prodigal abundance. At any one time behind the row on actual duty may be seen in reserve other rows of similar teeth that are in readiness to understudy the actual teeth whenever occasion may arise. There is thus provided a succession of teeth which continue throughout life to supply the demand for grasping organs (Fig. 37).

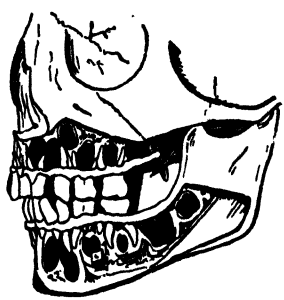


FIG. 43. — The two dentitions in man. The permanent dentition, which has not yet erupted, is shown in black. (After Sobotta and McMurrich. K. L. B.)

Through evolutionary processes this succession of one set of teeth after another has been reduced more and more until in man there is normally only one replacement, the *permanent dentition,* which supersedes the first set of teeth, or *milk dentition* (Fig. 43).

The fact that a part of the permanent dentition, the "wisdom teeth," is very often late in appearing, or indeed may fail to appear at all, indicates that humankind is still in the grip of regressive evolution so far as the succession of teeth is concerned.

3. DIGITAL TIPS

Among the most conspicuous reminders of an invertebrate exoskeleton to be seen in man are the *nails* which protect the fingers and toes.

Nails are of epidermal origin and are in fact quite as lifeless, when once they are formed, as the exoskeletal crust of a crustacean. Like the invertebrate exoskeleton they are periodically discarded in fragments and constantly renewed.

Between the outermost dead corneal layer of the epidermis and the deep-lying germinative Malpighian cells there are certain transitional cells forming the *stratum lucidum* (Fig. 36). These cells, which are likewise derived from Malpighian cells, make up the nails. To this end they fuse together into a compact mass in which all original cell-boundaries are lost, so that consequently they do not scale off in separate corneal fragments to be loosened up and cast off as happens in other regions of the skin.

That part of the Malpighian layer which underlies the white half-moon, or *lunule* (Fig. 44) that shows at the base of the nail, is the chief source of its continuous renewal. From this region new nail-forming cells are constantly pushed not only outward but also forward toward the finger-tip. In all other regions of the skin, it will be remembered, the renewing cells from the Malpighian layer in the course of their metamorphosis are simply pushed outward.

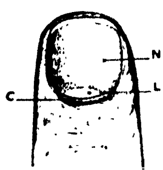


FIG. 44. — Tip of finger. *N*, nail; *L*, lunula; *C*, corneum encroaching upon the nail at its base.

The rate of nail growth, which may be easily noted whenever one establishes a landmark for reference by accidentally hammering a finger-nail, is roughly an inch in six months. If never trimmed or broken, nails ought

theoretically to be over ten feet long when man reaches the alloted age of three score and ten.

The pinkish aspect of the nail beyond the white lunula at its base, where the Malpighian layer underneath is of extra thickness, is due to its semi-transparency which allows the blood to show through.

The relation of the nail to other parts of the skin is made evident in Figure 45.

The whole nail pushes out through the dead corneal layer of the skin, which may be seen encroaching over the lunula and at the sides as well as underneath the projecting edge of the nail where dirt collects. The refinement of manicuring consists largely in attending to this ragged frame of corneum in which the nail itself is set.

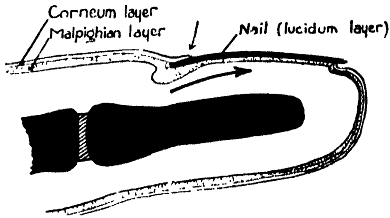


Fig. 45. — A diagram of a long section through a finger-tip, showing the relation of the corneum and the Malpighian layer to the nail. The large arrow points the direction of growth and the small arrow indicates the lunula region where the Malpighian cells are most active.

The device of a horny digital-tip has been differentiated into various modifications to fit diverse needs, particularly among the higher vertebrates or mammals. For instance, among the larger animals, that never sit down but are on their feet much of the time, the nails are in the form of thick shoe-like *hoofs* which furnish the necessary firm foundation for these big organisms. The carnivores, on the other hand, have *claws*, which are like nails that have been pinched together laterally and

drawn out to a point. These claws are suitable for the bloody business which Nature's flesh-eaters have in hand. They may be retractile and thus kept sharp, as with certain cat-like beasts of prey, or they may be stout and exposed and consequently useful for the purpose of digging, as in the case of those animals which entrench themselves in holes and burrows.

The flattened nails of man serve to reinforce and protect the sensitive finger-tips which play a rôle of incalculable importance in his daily life.

All of these different digital-tips, however, are homologous and may, therefore, be interpreted as various expressions of a single plan.

4. Hair

a. Other Epidermal Structures

There are other epidermal structures to be found elaborated in various vertebrates, such as *horns* and *antlers* of hoofed animals, the "*whalebone*" of whales, *feathers* of birds and the great variety of horny lips, or *beaks*, of birds and turtles; but as none of these structures has ever been appropriated by evolving man for his own use they may be passed by here. There remains to be mentioned, however, one other protective epidermal device that is characteristic not only of man but of all other mammals as well, namely, *hair*.

b. Origin

Hair is entirely epidermal in origin. It arises, as all epidermal structures arise, from the active increase and elaboration of cells in the Malpighian layer of the

epidermis and, like other dead epidermal parts, in the natural course of events it is molted and is periodically renewed. Moreover, it is a protective covering, and

FIG. 46. — Face of a five months' old embryo with temporary hairy covering (lanugo). (After Ecker, in Wiedersheim's "Structure of Man." Macmillan.)

hence by it we are again reminded of the protective exoskeleton of invertebrate animals.

c. Distribution

Primitively hair clothes nearly the entire body, as shown typically by the pelt of any fur-bearing animal. Even man during embryonic growth passes through a fur-bearing stage when soft, delicate fetal fur, ***lanugo***, covers all of the body except the red part of the lips,

the external genitalia, the digital tips already covered by the nails, the palms of the hands and the soles of the feet (Fig. 46). Before birth, however, this temporary lanugo practically vanishes, to be replaced by another covering of hair which is much less general in its distribution and which becomes locally accentuated at puberty. It is renewed periodically throughout life with varying fortunes, particularly that part thatching the top of the head.

d. Anthropology of Hair

Although man is less hairy than any of his mammalian cousins, the microscope reveals, as a reminder of ancestral times when hair was the common means of protection, rudiments of hair even on those areas of the skin where it is apparently absent.

But although hair in general is plainly in the list of degenerate and vanishing structures, an exception must be made in the case of the beard of the human male. This is a progressive and modern character in the evolutionary sense, absent among monkeys and apes and undeveloped among primitive races. Moreover as the beard becomes differentiated in the higher races of man, at the same time correlatively the hair of the head of the female becomes longer and that of the male shorter.

But in general hair, along with other epidermal structures mentioned in this chapter, represents anatomical relics of a bygone age, which must be regarded as vanishing makeshifts of ever lessening importance to the evolving human machine.

CHAPTER V

THE OLDEST PART OF THE SKELETON

1. THE MAIN SKELETAL AXIS

In the group of higher animals to which man belongs there is always one bodily dimension which is considerably in excess of all others. This obvious condition, which is so self-evident that it ordinarily fails to stimulate thought, is the result of a long series of evolutionary adaptations.

The most primitive shape for an animal or a plant is that of a sphere in which all diameters are alike. Microscopic examples of such organisms are to be found today living suspended in water and moving with equal facility in any direction. The sphere is likewise the typical form for an egg, spore or ovule. It is, therefore, the initial shape assumed by practically all animals or plants, even those which may attain most diversified forms when fully grown.

Out of this primitive spherical form two great types of bodily symmetry have been evolved, namely, the *radial* and the *bilateral*.

The radial type is adapted to stationary existence and is best exemplified by plants which need to reach out equally in every direction because they are attached to one place.

Ordinarily the elongated bilateral type exhibits organs of locomotion on either side of the body and a directive

head in front. Thus locomotion with a profitable change of locality is gained most effectually by having one axis of the body exceed all others.

The elaboration of the bilateral type of symmetry reaches its highest expression in the vertebrates, in which group the long dimension of the body is stiffened by a *skeletal axis* lying between two tubes that similarly

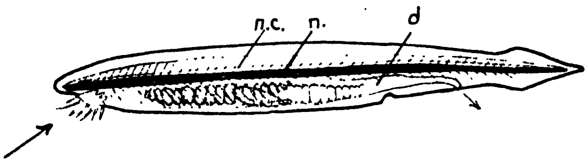


FIG. 47 – Outline of *Amphioxus*, in which the vertebrate plan of structure is reduced to its lowest terms. *n..c*, nerve-cord; *n*, notochord; *d*, digestive tube.

run lengthwise the body (Fig. 47). The *digestive tube* which lies below the skeletal axis, is ordinarily much longer than the body itself, and consequently is more or less coiled. It is open at either end, that is, at the mouth and at the anus, and constitutes the highway through which the food passes.

The *neural tube* on the other hand, which lies above the axis, is relatively short and straight. It is closed at either end and lies almost in contact with the skeletal axis itself. As a matter of fact, parts of the skeletal axis grow around, encasing it protectively. At one end the neural tube, or as it is commonly called the spinal cord, expands into the brain around which the skeletal axis has also developed a protective case called the *skull*. Thus the skeletal axis, which is made up of the back-

bone and the skull, is seen to hold intimate and fundamental relations with the nervous and digestive systems and to have been evolved primarily to meet the mechanical necessities arising from a locomotor bilateral type of bodily symmetry.

2. A Typical Vertebra

Among the vertebrates the skeletal axis is composed for the most part of separate bony elements, or *vertebræ*,

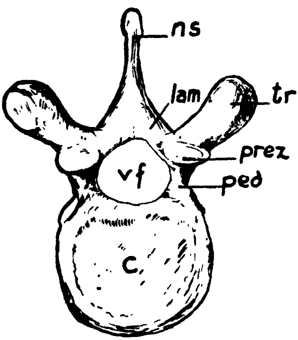


Fig. 48. — The tenth thoracic vertebra as seen from above. *c*, centrum; *lam*, lamella; *ns*, neural spine; *ped*, pedicel; *prez.*, prezygapophysis; *tr*, transverse process; *vf*, vertebral foramen. (After Spalteholz.)

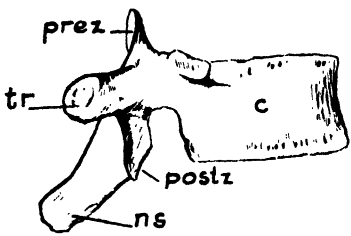


Fig. 49. The tenth thoracic vertebra as seen from the right. *c*, centrum; *ns*, neural spine; *prez*, prezygapophysis; *postz*, postzygapophysis; *tr*, transverse process. (After Spalteholz.)

which lend to the entire structure a certain degree of flexibility without sacrificing the stiffening quality for which the "backbone" stands.

The parts of a typical vertebra are (1) the centrum, (2) arch, (3) processes and (4) foramina as shown in Figures 48 and 49.

The *centrum* is the body of the vertebra upon the dorsal or posterior side of which is saddled the *neural arch* through which the nerve-cord is safely conducted. The neural arch is a composite structure made up of two *pedicels*, or columns, that pass over continuously into two flattened *lamellæ* which converge like a roof until they meet at the ridgepole above to form the *neural spine*.

In many vetebrates with well-defined tails a second arch, known as the *hæmal arch*, is present on the opposite, ventral side of the centrum, affording a protected passageway for the large blood-vessels that supply the tail region (Fig. 50).

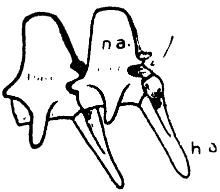


Fig. 50. — Two tail vertebræ of an alligator showing hæmal arches *h.a.*, hæmal arch; *n.a.*, neural arch. (After Kingsley.)

Extending in various directions from the neural arch are seven outgrowths, or *processes*, which offer convenient surfaces either for muscle attachment or for frictional contact of one vertebra upon another.

One of these seven processes, the *neural spine* already mentioned, forms the keystone of the arch, while two others, the *transverse processes*, which are located at the junction of the pedicel and the lamella on either side respectively, project laterally somewhat like the exaggerated eaves of a Chinese pagoda.

On the sides of the pedicels are four more processes bearing articular surfaces. The two anterior of these, *prezygapophyses*, are on either side, face upwards, and the two posterior ones, *postzygapophyses*, face downwards.

The articular surfaces of the prezygapophyses of any given vertebra rest upon the corresponding articular surfaces of the postzygapophyses of the vertebra next in front, and thus a certain amount of movement between the vertebræ is made possible (Fig. 51).

Movement, it should be remembered, depends upon muscles and joints. In those regions of the backbone, therefore, where movement is most needed, as for instance in the neck, the various processes of the vertebræ are most elaborated. On the other hand, where rigidity and the absence of movement are desirable, as for example in the sacral region, all processes are much reduced.

Furthermore, certain *foramina* or passageways are present in the vertebral column, notably the large neural foramen formed by the neural arch in which the nerve-cord lies, and the spinal foramina (Fig. 51) between the vertebræ themselves, through which the trunks of the spinal nerves as well as certain blood-vessels, find egress.

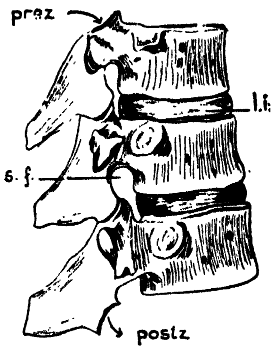


FIG. 51.—The tenth, eleventh and twelfth thoracic vertebræ taken from the right to show their articulation by means of zygapophyses. *s.f.*, spinal foramen; *l.i.*, ligamenta intervertebralia; *prez*, prezygapophysis; *postz*, postzygapophysis. After Spalteholz. (W. P.)

Finally, all of the parts which constitute a typical vertebra undergo the widest variation in different species of vertebrates and even in the different vertebræ that make up the backbone of any individual.

3. The Number of Vertebræ

In mankind the number of vertebræ making up the backbone does not increase with age and growth but, on the contrary, in consequence of fusion which may occur at about twenty-five or thirty years of age, the separate elements of the backbone become fewer in number in adult life than in infancy, as shown in the table below.

Kind of Vertebræ		Number	
		Infant	*Adult*
True	Cervical	7	7
	Thoracic	12	12
	Lumbar	5	5
False	Sacral	5	1
	Coccygeal	4 or 5	1
	Total	33 or 34	26

The consolidation of the sacral vertebræ, which results in increased ridigity and an improved mechanism for supporting the weight of the body upon the legs, has doubtless a different history behind it than has the fusion of the coccygeal vertebræ, which represent the remains of a vanishing ancestral tail. In the former case the fusion, to Lamarckian eyes at least, appears to result from use, and in the latter instance from disuse.

4. The Relation of the Vertebræ to Each Other

The separate vertebræ play upon each other at friction surfaces, or *articulations*. They are held together by means of *ligaments* and are moved by elastic *muscles*.

a. Joints

Articulations between the vertebræ, or joints, are of two kinds; those between the centra and those between the processes, that is, between the *zygapophyses* arising from the arches saddled upon the centra.

In man the articular surfaces of the centra are practically flat and are prevented from coming into direct contact with each other by a padding of compressible fibrous cartilage known as the intervertebral discs, or *ligamenta intervertebralia* (Fig. 51). Since the surfaces of the centra are not friction surfaces and, therefore, do not move upon each other in true joint fashion, whatever movement occurs at those points is accomplished by the compression and recovery of these discs.

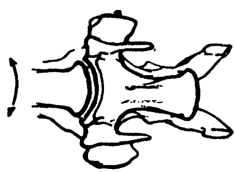


FIG. 52. — Ventral view of one cervical vertebra and a part of another of a swan, showing a saddle-joint, the movement of which is not only in the direction of the arrows but also at right angles to them. (K. L. B.)

In various lower vertebrates, however, friction surfaces do exist between the centra of the vertebræ. Such articulations between centra may be in the form of ball-and-socket joints, like those of snakes which gain considerable flexibility thereby; or, as exemplified in the necks of birds (Fig. 52), they may occur in the form of saddle-joints, moving freely in two general directions, either forward and backward or from side to side. A man astride a particularly hollow-backed saddle-horse illustrates the action of a saddle-joint.

In most fishes the centra are hollowed out at either

end (Fig. 53), fitting together rim to rim in a way that allows very little flexibility throughout the whole vertebral column, a condition which admirably serves the uses of a fish as it sculls its way through the comparatively dense medium of water with its stiff rudder-like tail.

FIG. 53. — A diagrammatic long section through a piece of the backbone of a fish showing the centra, hollow at either end, and the surrounding connective tissue sheath.

The most efficient intervertebral articulations are those between the processes or zygapophyses of the vertebræ. These are absent in fishes but they gain more and more prominence in the ascending vertebrate series until in man they form the principal true joints between the vertebræ. Similar friction surfaces are present upon the centra and transverse processes of the thoracic vertebræ for the purpose of articulating the ribs with the vertebral column.

b. Ligaments

The separate vertebræ are held together as a stiffened unit, or column, by many tough ligaments and elastic muscles. Most of these connecting elements are short, knitting together the vertebræ from centrum to centrum, from arch to arch and from process to process. Two, at least, the *ligamentum longitudinale anterius* and the *ligamentum longitudinale posterius*, extend virtually the entire length of the vertebral column along the anterior (ventral) and the posterior (dorsal) sides of the centra, uniting them all together. The *ligamentum nuchæ*, in the manner of an elastic check-rein on a horse, helps to connect the vertebræ of the neck with the skull. Thus, al-

though the vertebral column is composed of separate parts yet these units are all interdependent and not only so but they are intimately bound together as well into an organic whole.

5. The Manner of Origin of the Vertebræ

a. The Notochord and its Sheaths

The formation of vertebræ in the embryo is preceded, in the case of every backboned animal, by a temporary skeletal axis called the *notochord*.

The position of this temporary axis, which lies lengthwise between the neural cord and the digestive tube, is the same as that of the succeeding vertebral column. The notochord, in fact, takes part in the actual formation of the vertebral column.

At first the notochord cells (Fig. 2) are relatively large with thin walls, quite unlike ordinary skeletal tissues in which the cell-walls are excessively developed. Whatever rigidity the notochord possesses is due principally to the fact that its cells, instead of elaborating heavy walls, are crowded closely together within a tough unyielding notochordal sheath. In much the same way certain sausages have a turgid stiffness because the fragments of meat composing them, although soft and unyielding in themselves, are crammed immovably into a casing.

As the notochord grows older, the cells within the sheath change. Some of them crowd next to the sheath to form a layer of peripheral notochordal cells while those in the center tend to lose their outlines and to fuse together.

The peripheral notochordal cells then become transformed into a second sheath inside the primary one (Fig. 2), so that the notochord as a whole at this stage might be described as a cylinder of closely packed cell-remains surrounded by a double sheath and tapering at either end.

In Amphioxus (Fig. 47), that much studied Adam and Eve of all the backboned animals, in which the vertebrate plan of structure is expressed in its lowest terms, the

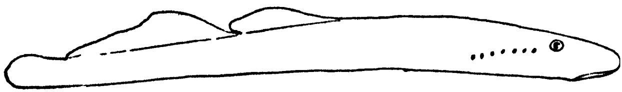


FIG. 54. -- A lamprey eel, whose "backbone" is a notochord.

vertebral column evolves no further than the notochordal stage throughout life. Certain primitive fishes, the cyclostomes, of which the lamprey eel (Fig. 54) and the hagfish are examples, show a similar simple stage of development of the vertebral column. In other vertebrates, however, the notochordal stage is passed through and an axial skeleton of another more complicated kind is attained.

The notochord is, therefore, the oldest part of the vertebrate skeleton antedating all other skeletal tissues not only during the development of the individual but also throughout the long evolution of the vertebrate type.

b. The Formation of the Neural Arch

Although *support* in the form of a stiff rod through the long dimension of a bilaterally symmetrical animal is

thus seen to be the earliest function that any skeletal tissue in a vertebrate performs, the function of protection, particularly of the precious nerve-cord lying just above the notochord, begins to appear very soon after.

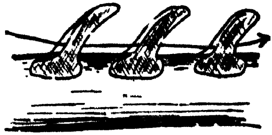


FIG. 55. — Diagram of a piece of the notochord of a lamprey eel with cartilaginous arches, indicating the beginnings of vertebræ, saddled upon it. The arrow shows the position of the nerve-cord.

Even in the lamprey eel (Fig. 55), pairs of small cartilage plates arrange themselves along the notochord on either side of the nerve-cord. Although they do not meet in a keystone above, they foreshadow the future neural arches of the higher vertebrate type. In later evolutionary stages most fishes as well as other vertebrates above them exhibit these plates joined above, thus establishing the neural arch.

FIG. 56. — Ball-and-socket vertebræ of an adult alligator, showing the suture between the centrum and arch still persisting. (R. S. S.)

No trace of the fusion which has taken place between arch and centrum is to be seen as high up in the evolutionary series as the vertebræ of an adult human. The original separateness of the two parts, however, is clearly established not only by the evidence of embryology but also by that of comparative anatomy, since distinct sutures between the arch and the centrum of the vertebræ appear, for example, in the young child, in adult alligators (Fig. 56) and in turtles.

c. The Formation of the Centra

Soon after the arches begin to form around the nerve-cord the notochord commences to transform itself into the centra of the future vertebræ. Rings of cartilage appear around the notochord just outside the notochordal sheaths and opposite the paired cartilaginous plates that are forming the neural arches. Each cartilage ring is destined to form the centrum of a future vertebra. As these cartilage rings grow more on the inside than on the outside they gradually pinch into, or invade, the cylindrical notochord. Figure 57 shows diagrammatically a long section through the notochord at this stage.

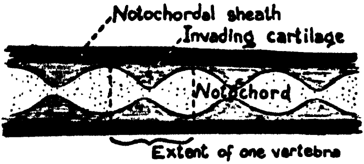


FIG. 57. — Diagram of a long section through a developing backbone at the stage when the notochord is being invaded by cartilage rings to form the centra of the vertebræ.

The result of this process is that the cartilage rings are eventually transformed into the centra of the vertebræ, becoming hollow at either end and fitting together rim to rim, while the space left within the hollow ends of the vertebræ is still filled with the remains ot the vanishing notochord.

This embryonic stage of the centrum corresponds exactly with the typical condition found in adult selachian fishes, such as the dogfish, where the vertebræ fit together like spools placed end to end, articulating by their centra and held together in a column by a common sheath while at the same time a secondary protective

covering made up of a more or less complete system of arches is placed along the dorsal side of the vertebral column to roof in the nerve-cord.

This cartilaginous invasion of the notochord, which results in the permanent cartilaginous centra of such fishes as the dogfish, is followed in the case of most vertebrates by the downfall of cartilage before the gradual encroachment of bony tissue. The final result is a bony centrum, the last and most efficient of three dynasties of tissue serving as a skeletal axis.

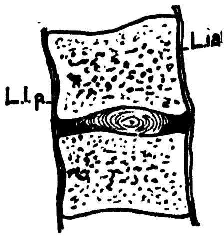


FIG. 58. — A long section through the centra of two vertebræ and an intervertebral disc in the center of which the last remains of the notochord shows as the *nucleus pulposus*. *L.l.a.*, ligamentum longitudinale anterius; *L.l.p.*, ligamentum longitudinale posterius. (After Gegenbaur.)

In the vertebræ of human adults a trace of the embryonic notochord still remains in the shape of the *nucleus pulposus* (Fig. 58) that forms the central core of the *ligamenta invertebralia* which occur between the centra of all true vertebræ that do not become fused together.

Not only is this succession of tissues in the formation of the vertebræ gone through with in the development of each human being, but there are animals living to-day that in their adult condition picture each stage through which the individual thus passes. So it is that comparative anatomy brings confirmatory evidence to the story of embryology, and embryology in turn helps to explain the anatomical differences which obtain among our animal kin.

6. The Kinds of Vertebræ

While all the separate vertebræ composing the backbone are easily referable to one structural plan, no two are exactly alike. The variations that have arisen are closely correlated with the diverse work which each vertebra, or group of vertebræ, has to do. Thus, since it is desirable to have the head movable in any direction without the trouble of turning the entire body, the vertebræ of the neck which carry the head have developed joints that move more freely than any to be found elsewhere in the skeletal axis. On the other hand, the sacral vertebræ, which bear the weight of the body upon the legs, have lost their movable joints entirely and have become fused together into an efficient unit for support.

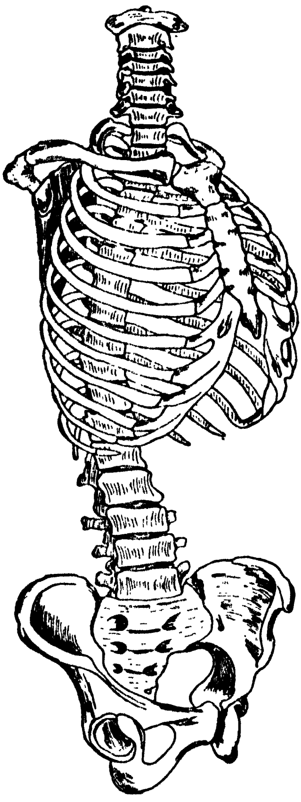


Fig. 50. — The backbone, thoracic basket and girdles. (After Sir Chas. Bell, 1818. W. P.)

The points of attachment of arms and legs, as well as the region where ribs are present, serve as landmarks to divide the vertebral column into five natural groups

of vertebræ, namely, cervical, thoracic, lumbar, sacral and caudal (Fig. 59). These five groups will be briefly considered in order.

a. The Seven Cervical Vertebræ

In the case of all mammals, with two or three exceptions [1] to prove the rule, there are present seven cervical vertebræ whether the neck is functionally absent as in whales or conspicuously present as in the bizarre giraffes.

A cervical vertebra (Fig. 60) may be easily identified by the large *foramen transversarium* penetrating it on either side at the base of the transverse processes. Through these foramina pass the vertebral arteries and veins as well as certain nerves. The manner in which these foramina came to be formed will be referred to later in connection with a consideration of the ribs.

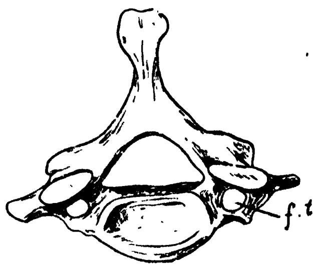


FIG. 60. — The seventh cervical vertebra (vertebra prominens) showing on either side the *foramen transversarium* (*f.t.*). (After Spalteholz.)

Considerable structural modification is shown by the cervical vertebræ due to a certain amount of division of labor among them. The relatively enormous skull rests upon the first cervical vertebra, commonly known as the *atlas* (Fig. 61). Upon two articular surfaces at the base

[1] There are nine cervical vertebræ in the three-toed sloth (Bradypus) and six in the two-toed sloth (Cholœpus) and in the American sea-cow (Manatus).

of the skull, the *occipital condyles*, play two conspicuous articular surfaces of the atlas, allowing the forward and backward, or nodding, movement of the head. The atlas is virtually without the neural spine of a typical vertebra and it has also lost its true centrum. Its neural arch, however, is relatively large and, with a substitute bridge of bone where the true centrum ought to be, forms an open ring.

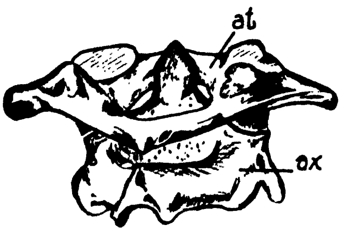


Fig. 61. — The human atlas (*at*) and axis (*ax*). (After Sobotta and McMurrich.)

The second cervical vertebra, or *axis* (Fig. 61), has a double centrum, its own and the lost centrum of the atlas which is fused with it, forming a large process, the *odontoid process* that projects toward the head. The odontoid process rocks back and forth and from side to side upon an articular surface within the ring of the atlas, thereby allowing lateral movements of the head. That this large process is really the transformed centrum of the atlas is borne out by the fact that it is in the position of the missing centrum of the atlas and also because in fetal life it is entirely separate from the axis. Furthermore, it is formed embryologically around the notochord as a core in the same way that the centra of other vertebræ are.

Thus the two joints, namely, that between the atlas and the skull and that between the atlas and the axis, provide for two of the most important movements of the head, that is, a forward and backward movement and one from side to side. The other cervical verte-

bræ take care of the twisting or rotary movements of the head so that the important sensory organs borne in it may be easily oriented in any direction for the convenient reception of environmental stimuli.

The neural spines of the cervical vertebræ from the second to the sixth are more or less forked, a modification more apparent in modern civilized peoples than among primitive races of man and his ape-like cousins.

In the seventh cervical vertebra the neural spine becomes larger than the other cervical spines. It is unforked and projects backward forming a noticeable landmark under the skin at the base of the neck when the head is bowed forward. For this reason this vertebra is sometimes termed the *vertebra prominens* (Fig. 62).

FIG. 62.—A profile showing the *vertebra prominens.*

b. The Twelve Thoracic Vertebræ

The thoracic vertebræ all bear ribs and consequently show articular facets for that purpose in addition to the regular intervertebral zygapophyses (Figs. 48 and 49). The first thoracic vertebra resembles the seventh cervical one while the succeeding members of the series gradually become larger and more like the lumbar vertebræ that follow them.

c. The Five Lumbar Vertebræ

The lumber vertebræ increase in length and width over those of the thoracic region, attaining the largest size

of any movable vertebræ in the entire column. The fifth lumbar is the largest vertebra of all and weighs

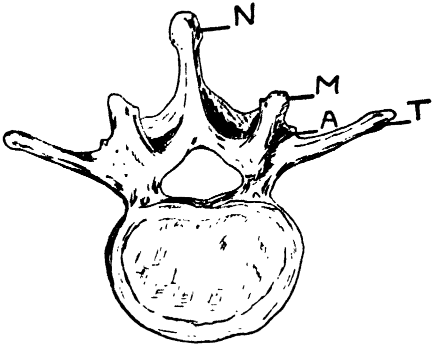


FIG. 63. — A lumbar vertebra. *N*, neural process; *M*, mammillary process; *A*, accessory process; *T*, transverse process. (After Sobotta and McMurrich.)

nearly as much as the seven cervical vertebræ taken together.

Although the lumbar vertebræ are without articular surfaces where ribs are attached, they are characterized by the elaboration of various other projections for the attachment of muscles, as, for example, the *mammillary* and the *accessory processes* shown in Figure 63.

d. The Five Sacral Vertebræ

The five sacral vertebræ fuse together with certain rib-like bony elements into a single wedge-shaped bone called the *sacrum* (Fig. 64), to which the pelvic arch is attached. The fact that the sacrum is made up by the fusion of five vertebral elements may be followed step by step in the growing embryo where the fusion

begins at the anterior end of the series and extends to the posterior region. Even in the adult individual the evidence of the compound origin of the sacrum is un-

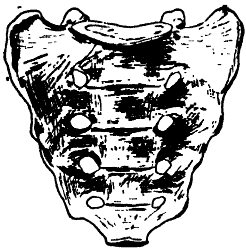


FIG. 64. — Anterior view of the sacrum.

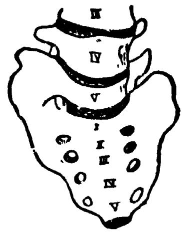


FIG. 65. An abnormal sacrum in which the fifth lumbar vertebra takes part. (After Frenkel.)

mistakable to the most casual observer. Sometimes the last lumbar vertebra becomes involved in the sacral fusion. Such an instance is pictured in Figure 65.

The part of the sacrum which furnishes the articular surface for the pelvic girdle changes with age. At first the last sacral vertebra furnishes the points of lateral contact but as development goes on this office is shifted anteriorly until eventually in adult life it is usually only the first two sacral vertebræ that function directly in this way.

The sacrum differs somewhat in the two sexes being broader, less curved, and pointed more obliquely backward in the female than in the male, a skeletal difference that has to do with adaptation to the function of childbirth.

e. The Vanishing Caudal Vertebræ

In man the tail vertebræ have undergone great degeneration, nevertheless, they are unmistakably present. The rudiments of as many as eight caudal vertebræ may be laid down early in the development of the human embryo but usually only four or five of these get as far as ossification. These degenerate vertebræ have lost their neural arches and the most of their processes. Only the diminishing centra remain.

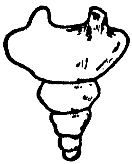


FIG. 66. – The human coccyx.

When the caudal vertebræ fuse together, as they customarily do in man, they form the coccyx (Fig. 66). Sometimes during middle life the coccyx even fuses with the sacrum.

The time will come when an inspired comparative anatomist will write a book of tails, in which the wonderfully diverse modifications of this interesting post-anal part of the vertebral column will be adequately set forth. He will have to describe and interpret the locomotor tail of fishes; the incorporated tail of the frog; the continuous tail of the snakes; the bludgeon tail of the alligators; the unwieldy tail of the stegosaurs; the supplemented tail of the birds; the amorous tail of the peacock; the supportive tail of the kangaroo; the trowel tail of the beaver; the ridiculous tail of the elephant; the flipping tail of the donkey; the swishing tail of the horse; the ornamental tail of the pig; the balancing tail of the cat; the grasping tail of the opossum; the reptilian tail of the rat; the emotional tail of the dog; and the lost tail of man.

7. The Human Vertebral Column

The units of the human vertebral column are more differentiated at either end than they are in the middle. At its anterior end noticeable specialization of the cervical vertebræ is correlated with use, while the degeneration of the caudal vertebræ is apparently an expression of disuse.

In a general way the entire skeletal axis has three uses, *support*, *protection of the nerve-cord* and *movement*.

a. Support

The function of support is what may be called the "backbone" function. In other words, it is the furnishing of a corner-stone upon which the other parts of the body are built. This solid foundation is arranged lengthwise the body along its longest axis because in this way the greatest number of bodily parts can conveniently be accommodated with a sustaining anchorage.

In animals like man which tip up on end and poise a heavy head on top of the vertebral column, the function of support is more effectually accomplished because of certain adaptive curvatures in the backbone (Figs. 59 and 144), which make the column mechanically stronger than a straight shaft would be. These curvatures, which are due more to modifications of the pad-like *ligamenta intervertebralia* between the separate vertebræ than to any direct change in the shape of the centra that are stacked one upon another, are less pronounced in infants and in primitive races than in an adult civilized man.

This is particularly true of the lumbar curvature (Fig. 67), which gives the typical hollow back to the well-formed man. Babies, which lack it, are flat-backed like their remote quadruped ancestors.

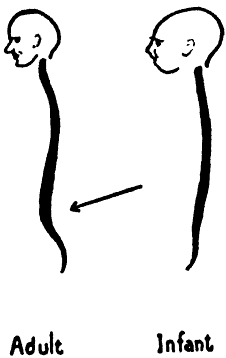


FIG. 67. — Diagrams showing the difference in the curvature of the backbone between an infant and an adult.

When kept in a vertical position, the entire skeletal axis shortens slightly during the day, owing to the compressibility of the ligamenta intervertebralia, which together make up approximately one-fourth of the entire length of the vertebral column. After a corresponding period of horizontal relaxation, which is usually spent in bed, the normal length is restored.

b. Protection of the Nerve-cord

The nerve-cord in vertebrates is an indispensable cable of great complexity, extremely delicate and liable to injury. It is not only ensheathed in its own envelopes, the *pia mater*, *arachnoidea*, and *dura mater*, but it is also surrounded by a protective jacket of fluid and furthermore encased within a bony conduit formed by the neural arches of the vertebræ. Even the backbone itself is overlaid with ligaments and is buried with its valuable contents protected from outside injury by surrounding muscles and fatty tissues. Finally the whole internal mechanism is effectually sealed up within the tough, resistent, practically germ-proof skin.

The human spinal cord is considerably shorter than the neural tube in which it was made to lie, ending in adult life, in fact, at about the level of the first or second lumbar vertebra. In other words, the nerve-cord has become more differentiated than the vertebral column.

c. *Movement*

Vertebral movement is, of course, confined to the free cervical, thoracic and lumbar vertebræ.

While it is relatively slight between any two particular vertebræ, when taken all together it amounts to enough to be greatly missed by anyone afflicted with a stiff neck or a lame back.

CHAPTER VI

THE THORACIC BASKET

1. Parts of the Thoracic Basket

The last chapter had to do with the backbone, that part of the skeleton which surrounds and protects one of the two important tubes which run lengthwise the body of every vertebrate, namely, the *tubular nerve-cord.* The other essential tube that characterizes the body of bilaterally symmetrical vertebrates is the *digestive tube,* and this is likewise encircled and protected at least partially by another part of the skeleton, the *thoracic basket,* which it is the purpose of this chapter to describe.

The bones making up the thoracic basket (Fig. 68) are the *thoracic vertebræ,* the *ribs,* the *sternum* and secondarily the *clavicles* and *scapulæ* of the pectoral girdle.

2. Contents

These parts unite together to form a basket-like structure which is hung firmly upon the upper half of the skeletal axis and encloses a considerable part of the digestive organs as well as other soft viscera in great need of skeletal protection, notably the heart and lungs (Fig. 69).

Still other organs were originally contained therein, but during the development of the individual, as well as in the course of the evolutionary history of the race, the basket has lost some of its contents. This change has come about in two ways; first, through shrinking of the

basket itself due to degeneration, particularly in the posterior region, and second, for the reason that certain organs, such as the kidneys, the small intestine and the internal reproductive organs, have migrated tailward

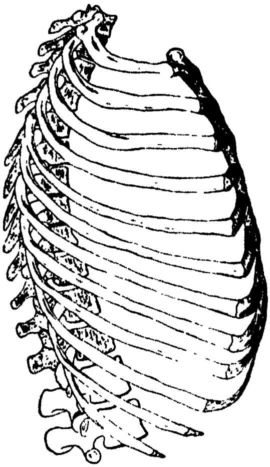


FIG. 68. — The thoracic basket. (After Spalteholz.)

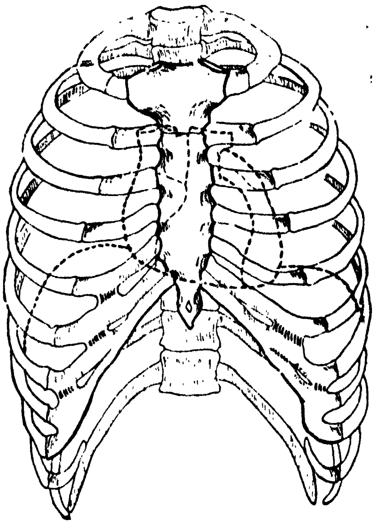


FIG. 69. — Diagram showing the position of the heart and diaphragm in relation to the thoracic basket. (After Spalteholz. W. P.)

from their original embryonic or ancestral positions within the basket.

Of all these changes the migration of the human reproductive organs is the most pronounced. The ovaries, which produce the eggs, have moved down to occupy new stations within the pelvic basin (Fig. 59), while the testes, which produce the sperm-cells necessary for the fertilization of the eggs, have gone from a region far up

within the shelter of the basket not only down to the posterior limit of the enclosed space in which the viscera lie, but have even pushed their way out carrying the body-wall before them, so that they hang suspended within the scrotal sac entirely outside the crowded body cavity.

3. Apertures

The thoracic basket is perforated above and below. The opening at the top is in the form of a rather restricted aperture, the margin of which is determined by the first thoracic vertebra, the first pair of ribs and the upper end of the sternum (Fig. 70). Through this narrow passageway crowd, side by side, various pieces of apparatus which provide for much of the traffic between head and body, such as the *trachea*, connecting the imprisoned lungs with the outside world; the *œsophagus*, that gives the countersign to food and drink, placing it beyond normal recall; the *vagus nerves*, wandering far from their headquarters in the brain to supply distant viscera; the *carotid arteries* and the *jugular veins*, which distribute and collect the blood in the head; and the *thoracic duct*, that brings back into the confines of the venous system escaped white blood-corpuscles from their missions of mercy throughout the tissues of the body.

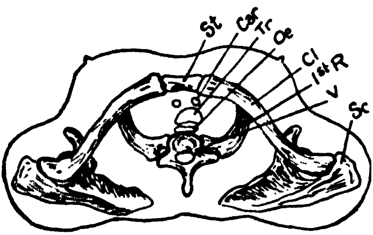


FIG. 70. — Diagram of the opening at the top of the thoracic basket as seen from above. *St*, sternum; *car*, carotid artery; *Tr*, trachea; *Oe*, œsophagus; *Cl*, clavicle; *1st R*, first rib; *v*, vertebra; *sc*, scapula. (After Witkowski.)

The lower aperture is larger than the upper one and is bounded behind by the last thoracic vertebra and the short twelfth pair of ribs attached thereto. The margins of the lower aperture on the sides and in front are determined by the tips of the tenth and eleventh pairs of ribs, by the cartilages of the other posterior ribs and by the lower end of the sternum. The aperture is closed crosswise by the vaulted diaphragm and it tends to slope downward from the sternum toward the backbone while the margin of the smaller upper aperture slopes upward toward the backbone. This is due to the fact that the thoracic basket is shorter in front on the sternal side than it is behind, by a ratio of about two to three (Fig. 68).

4. Shape

In general the form of the whole basket is somewhat cone-shaped with the smaller end toward the head.

The space within is partially divided into slightly enlarged right and left regions, because the column formed by the centra of the vertebræ stacked one upon the other stands out into the cavity, thus serving to a certain degree as a longitudinal partition. Within these lateral enlargements are packed the lungs while the heart, that wonderful automatic pump that must continue with unceasing regularity day and night as long as life lasts, is well guarded behind by the vertebral column and in front by the sternum. The heart, therefore, lies midway between the lungs instead of far over on the left side as melodramatic actors are wont to indicate its position (Fig. 69).

There are at least three kinds of variations which

normally occur in the shape of the thoracic basket. These are due to respiratory movements, to developmental causes and to sex.

With every breath the protective skeletal grillwork changes its form to which the lungs within intimately accommodate themselves. Not only intercostal muscles which crisscross between the ribs but also the yield-

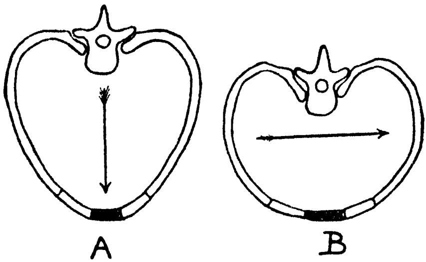


FIG. 71. — Cross sections through the thorax of a human embryo (*A*) and a human adult (*B*). The former resembles that of a quadruped. (After Wiedersheim.)

ing cartilages at the sternal ends of the ribs, the springy ribs themselves with their movable articular joints and the muscular diaphragm that stretches across the lower aperture, all interact together to make the thoracic basket an adaptable apparatus constantly varying in shape.

Again, when an embryo and an adult are compared in cross-section, the shape of the thorax shows decided variations (Fig. 71). In the embryo the dorso-ventral diameter is larger than that from side to side, a fact also true of quadrupeds. This condition is correlated in four-legged animals with the weight of the viscera pulling

mechanically from the backbone downward toward the sternum. In the human adult, however, where the visceral weight exerts a pull parallel to the backbone rather than at right angles to it, the greater diameter of the basket is no longer dorso-ventral but side to side.

Finally, variations associated with sex occur in the shape of the thoracic basket. The upper ribs of the female are more movable, the sternum relatively shorter and the superior aperture larger in proportion than in the male. This variation is largely an adaptation to modified respiration during pregnancy when the normal arrangement of the viscera in the body-cavity of the female is somewhat upset by the presence of the parasitic fetus.

5. The Ribs

The ribs, which have been documents of human interest ever since the days of the Garden of Eden, are the most conspicuous part of the thoracic basket.

There are twelve pairs of ribs in man (Fig. 68), although much evidence from comparative anatomy and from embryology support the conclusion that there were formerly more. In the two-toed sloth, *Cholæpus*, a primitive South American mammal, there are present as many as twenty-four pairs of ribs, while in the human embryo more than the normal twelve pairs of ribs are for a time present. Throughout the vertebrate series as animals became more specialized, the evolutionary tendency seems to have been toward a reduction of the number of ribs. That such a reduction is still going on in the case of man is evidenced by the degeneration of the ribs in

the posterior region of the thoracic basket where at least two pairs fail to reach the sternum.

To understand the nature of this degeneration it should be noted that in man all ribs articulate at one end with the thoracic vertebræ while at the other end only the first seven pairs, the *true ribs*, join the sternum. The remaining five pairs of ribs are known as the *false ribs*. Of these the eighth, ninth and tenth pairs anchor indirectly to the sternum by means of the cartilages of the seventh pair of true ribs while the eleventh and twelfth pairs, called the *floating ribs* (Fig. 144), have so far degenerated that they only partially encircle the body, thus failing to make even a vicarious attachment to the sternum.

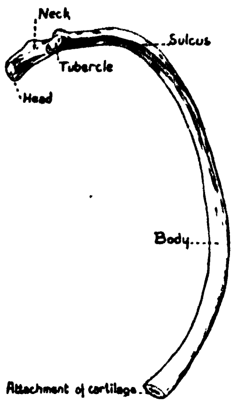


FIG. 72. – The fifth right bony rib, seen from below. (After Cunningham.)

The ribs in man, therefore, are seen to increase in length from the first to the seventh or eighth pairs and then successively to decrease to the twelfth pair, which may be reduced to mere stubs hardly more than an inch long.

In Figure 72 an isolated rib with its parts is shown. It is a flattened bone both bent and twisted so that it does not lie flat when placed upon a table. Its slender somewhat elastic body is pieced out at the sternal end with flexible cartilage. At the other end, which joins the thoracic vertebra in two places, are two prominences known as the *head* and the *tubercle* respectively, separated

from each other by the *neck* which is slightly narrower than the *body* of the rib. Both head and tubercle bear articular facets by means of which the rib plays upon its vertebral support

Between the head and tubercle of the rib and the vertebra with which it comes in contact there is formed, on either side, a sheltering passageway called the *vertebrarterial canal* (Fig. 73) through which run the ver-

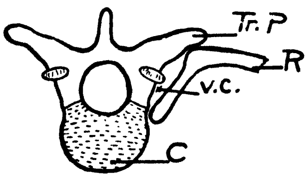


FIG. 73. — Diagram to show the articulation of a rib (*R*) on the centrum (*C*) and on the transverse process (*Tr.P*) of a vertebra, thus forming the vertebrarterial canal (*v.c.*). (After Weber. W. P.)

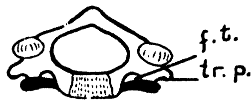


FIG. 74. — Diagram of a cervical vertebra showing how the *foramen transversarium* is formed by means of the remains of a cervical rib (in black). Compare with Fig. 73. (After Weber. W. P.)

tebral arteries. The *foramina transversarii* of the cervical vertebræ, mentioned in the last chapter, are formed much in the same way from the head and tubercle of embryonic cervical ribs of which nothing but the vertebral end remains (Fig. 74). Thus the vertebrarterial canal in the thoracic region and the foramen transversarium in the neck are homologous structures.

The tubercle of the rib, moreover, is to be interpreted as the degenerate remains of one arm of a Y by means of which the rib ancestrally articulated with the vertebra. The condition found in salamanders as shown in Figure 75 makes this homology clear.

Along the inner margin of each rib, for a part of its

length at least, is a shallow groove, the *sulcus*, shown in Figure 76, within the protection of which a vein, an artery and a nerve lie parallel to each other in harmonious safety.

The characteristic flatness of the ribs makes possible the attachment of the intercostal muscles, external and

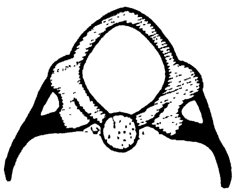


FIG. 75. — A vertebra and two ribs (in black) of a salamander showing the primitive double articulation of ribs to vertebræ. (After Gegenbaur.)

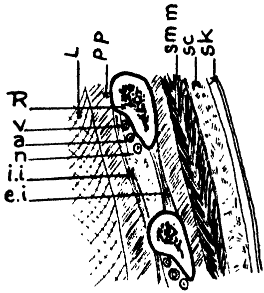


FIG. 76. — Diagrammatic section through the thoracic wall including two ribs. *R*, rib; *v*, vein; *a*, artery; *n*, nerve; *i.i.*, internal intercostal muscle; *e.i.*, external intercostal muscle; *L*, lung; *pp*, peripleural tissue; *sm.m.*, serratus magnus muscle; *sc*, subcutaneous; *sk*, skin. (After Tillaux.)

internal, as well as certain other muscles that have to do with respiration and the movement of the arms. The first pair of ribs, which is not only the shortest and most curved but also the stoutest, flattest and broadest of all the twelve pairs, on account of its location in the neighborhood of the arms furnishes attachment for at least a half dozen muscles, viz., the *intercostal external* and *internal*, the *levator costæ*, the *scalenus medius* and *anterior*, and the *serratus magnus*.

The very fact that the indispensable muscles which have to do with respiration, such as the *intercostals* or the *serratus magnus* and the *pectoralis*, are inserted upon the true ribs, indicates that the evolutionary reduction in the number and size of these ribs has, in the case of man, probably reached its limit, because natural selection will never allow the respiratory apparatus to fall below a certain minimum of efficiency. The same thing is not true of the false ribs, particularly the "floating" ones, which have much less or in some cases nothing to do with the mechanism of breathing. They are no longer under the saving hand of natural selection and are, in consequence, gradually disappearing.

Numerous variations from the normal conditions among ribs, degenerative changes, irregularities in bilaterality and the frequent presence of extra ribs, all go to indicate that the human thoracic basket is by no means a finished structure but that its evolution is still going on.

In medical literature there are cited numerous cases of extra ribs persisting in adult life either at the cervical or the lumbar ends of the thoracic series. Pilling gives an instance of a pair of ribs on the seventh cervical vertebra that completely encircled the upper aperture of the thoracic basket and joined the sternum quite in the manner of true ribs. Persistent cervical ribs are more frequently incomplete and fail of direct sternal attachment (Fig. 77). Even the first pair of thoracic ribs may sometimes be incomplete (Fig. 78).

Additional ribs are of more frequent occurrence on the first lumbar vertebra, however, than in the cervical

region. Extra lumbar ribs are called "gorilla ribs" because they represent the normal condition in gorillas and chimpanzees. Rabl examined six hundred and

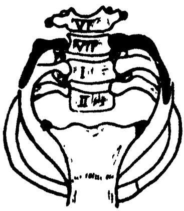


FIG 77. — Abnormal ribs (in black) on the seventh cervical vertebra of an adult individual. (After Leboucq.)

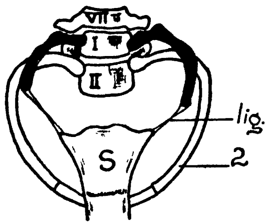


FIG. 78. — Reduction of the first pair of ribs (in black) in an adult individual. *lig*, ligament; *S*, sternum; *2*, 2nd thoracic rib; *VII*, seventh cervical vertebra; *I*, *II*, first and second thoracic vertebræ. (After Leboucq.)

forty bodies in the dissecting rooms at the University of Prague and found forty of them, or a little more than 6 per cent, with a gorilla rib on at least one side. On the other hand, it is interesting incidentally to know that two out of the six hundred and forty had only eleven pairs of ribs. Gorilla ribs are about three times more frequent in the male than in the female, a fact that is difficult to harmonize with Adam's historic loss and Eve's gain.

One case was reported by Rosenberg in 1899 of an individual with fifteen pairs of ribs, the extra ones being a pair of cervicals and two pairs of lumbars, while in fourteen out of seventy individuals, or 20 per cent of the number observed, the eighth pair of ribs on one or both sides was found, by another investigator, to reach the sternum directly as false ribs.

With respect to length the eleventh pair of floating ribs varies from six to eleven inches while that of the twelfth pair ranges from mere stubs to ribs which nearly

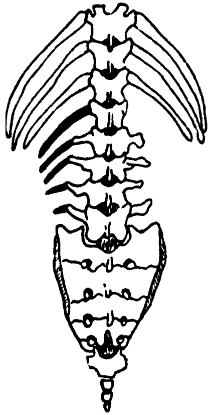


FIG. 79. — A part of the thoracic vertebræ; the lumbar vertebræ; the sacrum and the coccyx with embryonic lumbar ribs represented on one side in black. (After Wiedersheim.)

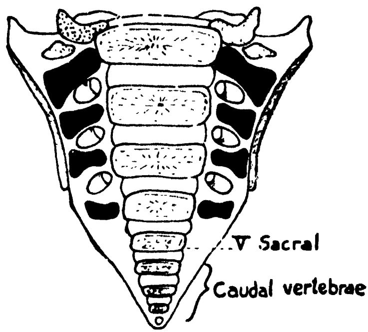


FIG. 80. — Sacrum of a five months' old human fetus showing sacral ribs (in black). (After Kollmann.)

encircle the body, or from less than an inch to nearly a foot.

Finally, there are in fetal life ribs temporarily present not only upon the seventh cervical vertebra but also upon all the lumbar vertebræ as indicated in Figure 79. Moreover, rib rudiments, which fuse afterwards with the transverse processes to form the lateral masses of the sacrum, are to be found attached to the sacral vertebræ (Fig. 80).

6. The Sternum

The *sternum*, or front bone as contrasted with the backbone, is the terrestrial part of the thoracic basket, that is, it first appears in evolutionary history in vertebrates that locomote upon land.

The need of such a strengthening structure to knit together the whole thoracic basket into a firm skeletal

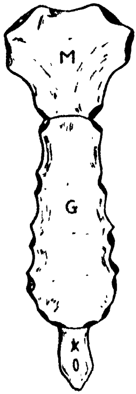


FIG. 81. The adult human sternu *M*, manubrium; gladiolus; *X*, phoid process (After Spalteholz.)

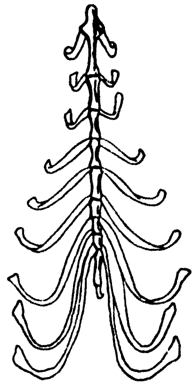


FIG. 82. The sternum and rib cartilages of a wolf, showing separate sternebræ (After Scott.)

unit to which the muscles of the anterior legs or arms may find suitable anchorage, is not felt by such primitive water dwellers as fishes that go forward by lateral tail motion rather than by the leverage of bilateral appendages. Neither is there a need for such a skeletal piece as the sternum in connection with the pelvic girdle and the posterior pair of legs because this apparatus,

unlike the corresponding pectoral girdle and the anterior pair of appendages, articulates at the sacrum directly with the vertebral column.

The sternum in the human adult (Fig. 81), consists of three parts, namely, the *manubrium* or head, and the *gladiolus* or body, both of which are formed of bones, and

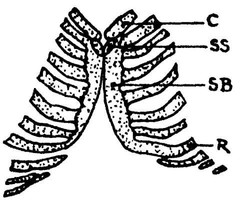


FIG. 83. - Ventral view of the developing sternum of a 30 mm. human embryo. *C*, clavicle; *SS*, supra sternal cartilage; *SB*, sternal bar; *R*, seventh rib. (After Ruge.)

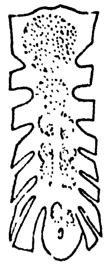


FIG. 84. - Sternum of a child showing centers of ossification. Seven ribs are attached on the right side and eight on the left. (After Markowski, in Kollmann's *Atlas*.)

lastly the *xyphoid cartilage*. In other mammals like the cow, sheep or wolf (Fig. 82) the sternum is made up, like the backbone, of a series of definite elements, *sternebræ*, separated from each other by intersternebral cartilages. Similarly in the human embryo the sternum is formed by a double chain of elements, made up at first of cartilage and later of bone, contributed from the cartilaginous ends of the ribs (Fig. 83). These elements eventually fuse together to make the adult structure.

The fact that two parallel centers of ossification occur

in the bony part of the sternum (Fig. 84), and that the xyphoid cartilage is frequently forked or perforated by a functionless foramen, is further confirmation of the bilateral origin of the sternum.

Sixteen articular surfaces or joints are present on the sternum (Fig. 81), twelve for the cartilages of the true ribs excepting the first pair which is fused to the sternum; two facets located upon the manubrium for the clavicles or collar-bones; one between the manubrium and the gladiolus; and one between the gladiolus and the xyphoid cartilage.

The last named joint makes it possible for the xyphoid cartilage, which hangs down like a tiny protective apron in the exposed notch on the front side of the thoracic basket, to swing outward and so accommodate itself to the displacement of the viscera behind it which is brought about by bending forward. If the xyphoid cartilage were to become ossified like the rest of the sternum and should be fused unyieldingly to the gladiolus, then every fat man would punch himself in the "pit of the stomach" every time he stooped over or sank into a seat.

The sternum is flat for the purpose of the attachment of muscles. In the case of bats and birds whose pectoral muscles are enormously enlarged for flight not only is the sternum considerably widened but a keel-like plate of bone, which vastly increases the available surface for the accommodation of muscles at a minimum expenditure of bony tissue, is also developed at right angles to the sternum itself.

Degenerative changes in the sternum are more pronounced in the female than they are in the male. They

are more evident in the region of the xyphoid cartilage than at the manubrial end, a condition that makes possible the expansion of the lower part of the thoracic basket during pregnancy. Moreover, about the region of the xyphoid cartilage the conservative effects of the respiratory muscles are little felt, while the same influence is more pronounced about the manubrium.

The shortening of the sternum which results in the formation of a conspicuous notch on the front side of the thoracic basket, is due principally to the fusion of the sternebræ, that is, the separate embryonic bones that make up the sternum, and the consequent disappearance of the intersternebral cartilages.

CHAPTER VII

EVOLUTION OF THE BRAIN CASE

1. The Complexity of the Human Skull

The human skull, which houses that most elaborated and useful mechanism, the brain, is itself the most complex part of the entire skeleton. The best avenue of approach to some understanding of the wonderful adaptations which it presents and to a partial appreciation of the beauty which marks its curving contours, lies not only in tracing its development as a part of the human skeleton but also in following through the skulls of the

Fig. 85. — Diagrammatic lateral view of the neurocranium and (in black) the splanchnocranium of the dog fish (After Jammes. J. W. W.)

ancestral types of vertebrates which have led up to its culmination in man.

The skull is a double structure, embryologically, morphologically and physiologically. *Embryologically* it is made up of two skulls of diverse origin, an outer and an inner, which supplement each other and in the course of

development come to fuse together into a harmonious whole. *Morphologically* one skull, the *neurocranium*, surrounds the brain end of the neural tube while another, the *splanchnocranium*, encircles similarly the anterior end of the splanchnic tube or digestive tract (Fig. 85). Finally, *physiologically* the two great fundamental functions of support and protection are equally provided for by the skull so that it may be said to serve a double purpose.

2. The Development of the Outer and Inner Skulls

A composite moving picture of the rise and union of the two embryonic skulls among vertebrates may, for arbitrary purposes of description, be divided into a series of stages which pass continuously from one into the next. Many of the following stages, which are largely represented by the adult condition in various vertebrates, extinct and living, are to be found, in counterpart at least, during the development of the human skull, although the parallel is by no means exact.

a. Notochordal Stage

Just as the brain is an evolutionary afterthought added to the spinal cord, so the first evidences of a future skull do not appear until after the notochord is well established. Before any skeletal elements except the notochord are present, a thin, tough membranous sac surrounds the brain which later gives rise to the *dura mater* and the roof of the skull. There are also three pairs of conspicuous sense-organs arranged one behind the other along the sides of the brain, the *ears*, *eyes* and *olfactory pits*

(Fig. 86), all of which migrate in from the surface of the head to be connected with the brain later by their respective nerves.

At this stage the anterior enlargement of the nerve-

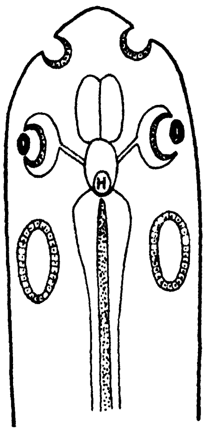


FIG. 86. — Diagram of the notochordal stage of skull development seen from the ventral side. The notochord (dotted) lies along the nerve-cord and brain as far forward as the hypophysis (*H*). Three pairs of sense-organs, nose, eye and ear, have appeared but as yet are without skeletal support. (After Wilder.)

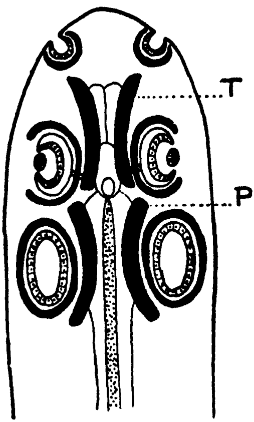


FIG. 87. — Diagram of the underpinning stage of skull development seen from the ventral side. The brain now rests upon the trabeculæ (*T*) and the parachordals (*P*) while each pair of sense-organs is supported by skeletal parts (in black). (After Wilder.)

cord in the form of the brain extends horizontally in front. Although in need of support, it is as yet quite unprovided for skeletally since the diminishing notochord

does not extend far enough forward and is not of the right shape to make a platform upon which the brain may rest.

b. Underpinning Stage

This need is soon met, however, by the appearance of two pairs of independent flat cartilages which form a primitive underpinning, or floor, for the support of the rapidly developing brain.

One pair of these cartilages, the *parachordals*, is placed under the brain with the posterior ends lying on either side of the notochordal tip end, while the position of the other pair, the *trabeculæ*, is more anterior as shown in Figure 87. Meanwhile delicate cartilaginous capsules partly enclose the three pairs of sense-organs.

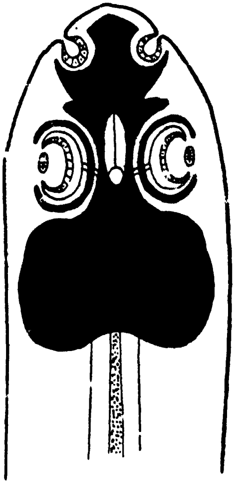


FIG. 88. — Diagram of the fusion stage of skull development seen from the ventral side. The parachordals and the trabeculæ, have fused together into a continuous platform involving the cartilage supports of the nose and ears and the end of the notochord, while those of the eyes remain independent in the form of the sclerotic layers of the eye-balls, thus making the movement of the eye-balls within the orbits, possible. (After Wilder.)

c. Fusion Stage

The four primitive girders thus laid down are at first quite independent not only of each other and of the end of the notochord but also of the six sense-organ capsules already present. Marginal growth speedily results in their coming into contact and eventually fusing together as a single continuous platform which encloses, at its posterior end, the tip of the

notochord and along its lateral margins the capsules of the sense-organs (Fig. 88).

This platform remains open in the middle, just anterior to the tip of the notochord in the region where the trabeculæ and the parachordals come together, and into the pocket thus left in the floor of the platform there fits a downward projection of the brain, the *hypophysis*.

The manner of fusion of this platform with the sense-organ capsules is different in the case of each, due to the fundamental difference in the kinds of stimuli which the various sense-organs are destined to receive. Thus the inner ear, which is attuned to respond to the vibratory contact of sound-waves that can be transmitted even through an enveloping case, is entirely surrounded by skeletal cartilage. The eyeball capsule, on the other hand, which needs to rotate freely in its socket in order to be directed towards vibrations of light coming from any direction, does not fuse with the rest of the skull at all but retains its independence, fitting within a socket, or orbit, formed in the wall of the skull. Consequently the primitive skeletal capsule of the embryonic eye eventually becomes the tough outer sclerotic coat of the eyeball. Finally, the capsules of the olfactory pits fuse solidly on the posterior and inner surfaces with the skull itself, although perforated by the olfactory nerves. In front they remain open like cups for the reception of odorous gases which, in order to produce a reaction, must come into direct chemical contact with the nerve-endings of smell within the cup.

d. Upgrowth Stage

The platform thus formed by fusion serves not only for support but also as a protection to the brain on its under side. The protective function is soon enlarged to include

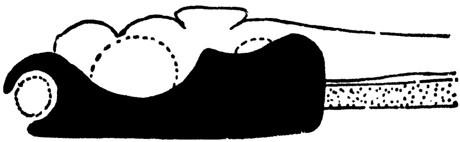


FIG. 89.—Up-growth stage of skull development as seen from the side. (After Roule.)

the sides of the brain by the upgrowth of the platform at its margins between the sense-organ capsules (Fig. 89). In this stage the skull somewhat resembles a deep spoon in the bowl of which lies the brain.

e. Roofing-over Stage

The growth at the margin of the enveloping cartilaginous skull-case continues until the edges meet and fuse together above, thus completing at least in primitive vertebrates a protective envelope on all sides of the brain. It frequently happens, however, particularly among higher vertebrates like man, that the roofing over is not accomplished with cartilage in the manner here described as characteristic for a primitive skull of the selachian fishes. For example, the skull of a selachian, like a dogfish, *Mustelis canis* (Fig. 90), is a continuous cartilaginous casket enveloping the brain with no sutures to demark separate elements. It is pierced by various small foramina through which the cranial nerves find

exit as well as by a large posterior opening, the ***magnum foramen***, through which the nerve-cord enters.

Thus far everything that has been detailed has to do solely with the formation of the inner skull. The stages

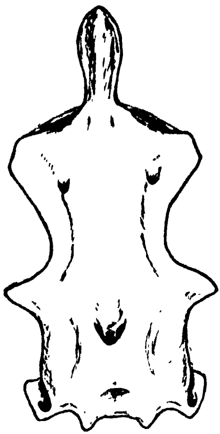


FIG. 90. — Dorsal view of the skull of a dogfish, showing a continuous cartilaginous capsule without sutures.

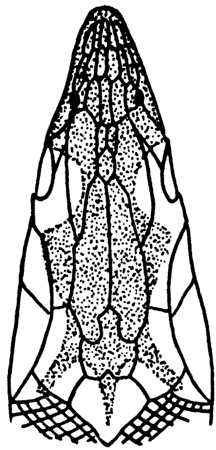


FIG. 91. — The skull of a sturgeon, *Accipenser*, showing the inner cartilaginous skull (dotted) and the outer skull of bony scales. (After Gegenbaur.)

that follow concern the origin of the outer skull, and the final modification and fusion of the two into one.

f. Shingling Stage

After the formation of the inner cartilaginous envelope just described, or even before the process is complete, the skull becomes partially overlaid with certain definite bony elements that are not first formed in cartilage and

which do not ordinarily fuse together so as to lose their identity, but which instead join each to the other by means of clearly defined immovable joints or sutures. These bones together constitute the *outer skull.*

In the cartilaginous ganoid fishes, such as the sturgeon, *Accipenser* (Fig. 91), these outer bones are small, numerous and quite scale-like in character. In fact they *are* the scales that cover the head and are in no way different, except in their somewhat enlarged size, from the

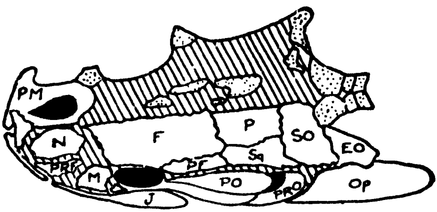


FIG. 92.—Skull of a ganoid fish, *Amia*, as seen from the dorsal side with the investing bones removed from the right half. *Investing* bones in white; Cartilage in parallel lines and *replacing* bones, ossifying out of the cartilage, dotted. *PM*, premaxillary; *N*, nasal; *PRF*, prefrontal; *M*, maxillary; *F*, frontal; *PF*, postfrontal; *J*, jugal; *PO*, postorbital; *PRO*, preopercular; *Op*, opercular; *Sq*, squamosal; *P*, parietal; *SO*, supraoccipital; *EO*, exoccipital. (After Bütschli.)

neighboring scales that cover the body. The outer skull then makes its initial appearance as an armor of separate scaly plates loosely shingled over the inner cartilaginous brain-box.

g. Ossification Stage

Centers of ossification soon appear in the inner skull, however, particularly around the foramina for the exit

of the nerves, where a protective function is doubtless served thereby, so that what was formerly a continuous cartilaginous sheath for the brain becomes replaced by definite bones.

These bones increase rapidly at their margins and so allow the entire structure to accommodate itself to the rapidly enlarging brain within, until finally the new bones join together in sutures as in the case of the scaly bones of the outer skull. Skulls in this stage of development occur principally among the bony ganoid fishes of which the bowfin, *Amia* (Fig. 92), is a representative. This process of ossification of the inner skull is more completely carried out in amphibia and reptiles.

h. The Union Stage

The outer skull-bones next sink deeper in from their former scale-like position, and, becoming overlaid with skin, are grafted inseparably to the bones of the inner skull. A single skull is now all that is visible for there is no way, except by tracing the mode of origin, to distinguish the *investing bones* of the outer skull from the *replacing bones* of the inner skull, since they both present the same appearance. This embryonic stage of the union of the outer and inner skulls is likewise represented in the evolutionary series among the amphibians and reptiles.

In all cases, however, the two skulls are not brought into so close contact with each other that the dual character of the vertebrate skull is obliterated. In the case of the turtle skull, pictured in Figure 93, the doubleness of the skull is still evident although the inner part

immediately around the brain and the large roof-like outer region do not correspond strictly to the "double skull" referred to in the preceding paragraphs

It will be seen that the size of the entire head is large in order to provide for the adequate attachment of the head muscles rather than to accommodate the brain which is disappointingly small. In fact the size of the entire skull is no true guide to the size of the brain within, since between the small inner skull that fits close around the brain and the vaulted outer skull there is a large vacant unused space like an unfinished attic in a house.

FIG. 93. — Back view of a turtle's skull, showing the false roof and large air-spaces over the part of the skull that immediately covers the brain. The magnum foramen is shown in black.

i. Bone-complex Stage

The final stage in either the development or the evolution of the human cranium is brought about by the fusion of neighboring bones into complexes that thereafter pass for single bones. Thus the *sphenoid* bone of the adult is a combination of at least ten embryonic bones, the *basi-* and *presphenoids*, which are represented throughout life in certain vertebrates as single bones, and the paired *orbitosphenoids*, *alisphenoids*, *pterygoids* and *median lamellæ*.

Since a light, strong brain-case is necessary in the

bird's skeleton for purposes of flight, the process of the formation of bone-complexes here has gone to such an extreme that most of the sutures of the skull become obliterated in adult life and consequently a bird's skull presents almost the appearance of a single bone.

In the case of the human skull, as previously intimated, all the evolutionary stages described in the preceding paragraphs are not repeated. The outer, investing skull, for instance, begins its rapid development before the inner cartilaginous skull is completed so that the upgrowth and roofing-over stages, in replacing of cartilaginous material at least, are rendered unnecessary with the result that they are omitted. There remain, nevertheless, unmistakable evidences of the dual origin of the outer and inner skull even in man.

3. The Splanchnocranium of the Dogfish

The description of the skull thus far given applies solely to the *neurocranium* which invests the end of the neural tube, that is, the brain. The other morphological half of the skull, namely, the splanchnocranium, surrounds the anterior end of the digestive tube primitively in the form of a series of cartilaginous arches.

Among the lower water-dwelling vertebrates the splanchnocranium is relatively large while higher up in the evolutionary scale it becomes more and more reduced. The converse is true of the neurocranium which increases in importance with the increasing size of the brain.

The primitive arrangement of the splanchnocranium may best be understood by reference to the skull of the dogfish (Fig. 85), where the distinction between the neu-

rocranium and the splanchnocranium is still perfectly evident

Here it will be seen that there are present seven cartilaginous arches arranged around the anterior part of the digestive tube one behind the other like horseshoes with the open ends up. Each arch is composed of a number of separate elements that articulate in a zigzag fashion so that the arch as a whole may be enlarged or contracted to some extent as occasion demands.

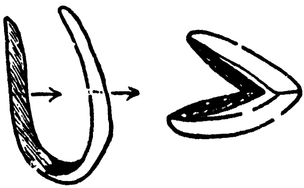


FIG. 94. — Diagram to show how the primitive upper and lower jaws form from a horseshoe-shaped cartilaginous arch.

The first or *mandibular arch*, which is the most anterior one, is made up of only four elements. These bend back forming a joint on either side and thus become the jaws, as shown diagrammatically in Figure 94.

The second, or *hyoid arch*, emancipated like the mandibular arch from bearing gills, is a suspensory apparatus since it furnishes the only points of articulation between the neurocranium and the splanchnocranium (Fig. 85).

The five posterior arches are *gill-arches* that hold open and, rib-fashion, protect the anterior end of the digestive tube. Between each of these pairs of arches are gill-openings which allow water entering the mouth to pass out on either side after bathing the vascular gills that hang suspended to the arches. Conditions essential for a respiratory mechanism, that is, circulating air in contact with moving blood with a semipermeable membrane between the two, are thus effectively secured for

these aquatic animals, since water contains air dissolved between its molecules, and gills are full of circulating blood exposed in thin-walled capillaries.

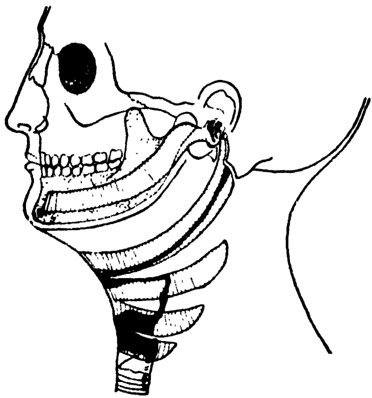


FIG. 95. Diagram to show the fate of the ancestral splanchnic arches in man. The arches are represented by the areas shaded with parallel lines and the parts of them which persist in adult man are shown in black. See table on page 112. (After Wiedersheim.)

The gill-arches diminish in size posteriorly and in bony fishes are fewer in number, the loss always coming at the posterior end of the series.

4. THE FATE OF THE SPLANCHNOCRANIUM

In the evolution of the vertebrates as the need for respiratory gills gave way before the rise of the lungs, the gill-arches became relegated to what may be called the anatomical scrap-heap.

There still persist even in man embryonic traces of

the primitive splanchnocranium in the form of three pairs of temporary and non-functional gill-arches that later vanish. Thus is the legendary history of remote

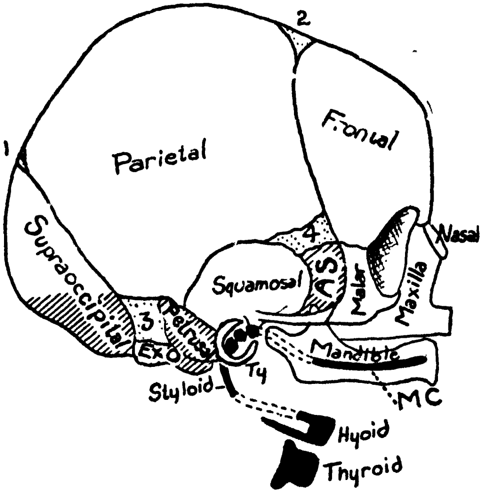


FIG. 96. — A fetal human skull. Derivatives of the splanchnocranium are shown in black; fontanelles by dotted, and cartilage bones by shaded areas. *Ty*, tympanic ring; *Ex.O*, exoccipital; *AS.*, alisphenoid; *MC.*, Meckel's cartilage; 1, occipital fontanelle; 2, parietal fontanelle; 3, mastoid fontanelle; 4, sphenoid fontanelle. (After McMurrich.)

ancestors retold in the human embryo. The gill-arches are not entirely lost, however, even in adult life, for certain parts of the mature skeleton are directly derived from the primitive splanchnocranium inherited from ancestral water-dwellers.

Nowhere is the thrift and resourcefulness of Nature better exemplified than in the disposal of the parts of the splanchnocranium after they have outlasted their origi-

nal use, owing to the emergence of vertebrates from life in water to land. What becomes of the different elements that make up the splanchnic part of the primitive skull is indicated in Figure 95 where the theoretical extent and position of the original arches are drawn as a background upon which are indicated the relics that persist.

The same thing is represented in Figure 96 and is also presented below in tabular form.

FATE OF THE SPLANCHNOCRANIUM

Number of Arch	*Selachians*	*Other Fishes*	*Amphibians*	*Reptiles and Birds*	*Mammals*
1	Upper and Lower Jaw	Palato-quadrate and Meckel's Cartilage			Incus, Malleus, Meckel's Cartilage
2	Hyoid Arch	Hyomandibular, Symplectic, Hyoid	Operculum, Columella, Hyoid Apparatus	Stapes, Hyoid Apparatus	Stapes, Styloid Process, External Ear Cartilage, Hyoid Apparatus
3	1st Gill-arch		Hyoid Apparatus		
4	2nd Gill-arch		Hyoid Apparatus	Missing	Thyroid Cartilage
5	3rd Gill-arch		Missing		Thyroid Cartilage
6	4th Gill-arch		Missing		Epiglottis
7	5th Gill-arch		Tracheal Cartilages		

It will be seen that the embryonic skeletal material which originally had to do with respiration and the support and protection of the anterior end of the digestive tube, has now by a complicated series of makeshifts assumed very diverse functions, as, for example, in connection with the support of the vocal apparatus and the muscular tongue, and with the transmission of sound-waves to the inner ear.

5. The Vicissitudes of the Vertebrate Jaws

In such fishes as the dogfish the first splanchnic arch serves the purpose of jaws in the manner already indicated. Its upper element on either side, which forms the upper jaw, is termed the *palato-quadrate cartilage*, while the lower element, constituting the lower jaw, is named *Meckel's cartilage* from a German anatomist with vision, Johann Friedrich Meckel (1781–1833), who first saw the cartilage in a human embryo (Fig. 96).

The cartilaginous splanchnocranium, in a manner similar to the process of development of the neurocranium, becomes overlaid in part by an outer bony splanchnocranium formed directly of plate-like elements which arise externally as scales do (investing bones), rather than as patterns of cartilage later copied into bony tissue (replacing bones). In this way the anterior part of Meckel's cartilage in the primitive lower jaw becomes encased with a number of investing bones. Some of these eventually bear the teeth, thus taking over the function that at first was performed by Meckel's cartilage alone. In the alligator's lower jaw these investing bones are still distinct, being separated from each other by definite

sutures (Fig. 97). In man they not only fuse together on either side but the two sides even unite into a single bone, the *mandible*. As these investing bones increase, Meckel's cartilage decreases until, in adult life, the latter has

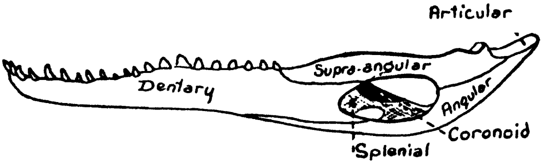


Fig. 97. — The lower jaw of an alligator, showing its six component bones. (After Schimkewitsch.)

entirely disappeared with the exception of its articular end which moves up into the neurocranium and becomes transformed into the second ear-bone, the *malleus*, of the middle ear-chamber.

The evolutionary history of the upper jaw is the same in principle as that of the lower jaw but it is somewhat more complex in detail. On the outside of the palato-quadrate cartilage in the lower vertebrates secondary investing bones form on either side, the *maxillary* and *premaxillary*, which bear the teeth and take over the function of the upper jaw. Meanwhile the palato-quadrate on either side ossifies into three bones, the *palatine*, *pterygoid* and *quadrate*, which, being relieved from the original work of the jaw, now become adapted to new uses. The palatine and the pterygoid tip over their flat surfaces from a vertical to a horizontal position, and, widening out to meet their fellows on the other side, move in to form the *hard palate* or the secondary roof of the mouth (Fig. 98). At the same time the quadrate still

persisting in its old position serves as the point of articulation for the lower jaw among most vertebrates. In the mammals, to which man belongs, the quadrate migrates up into the neurocranium as does also the ar-

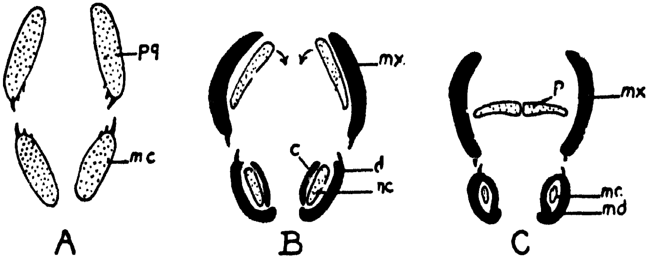


FIG. 98. — Diagrammatic cross-sections through the jaws looking down the throat of (*A*) a dogfish, (*B*) a bony fish, and (*C*) a mammal, to show the evolution of the mammalian hard palate (*p*) from the upper jaw (*pq*) of selachian fishes. *Pq*, palatoquadrate; *mc*, Meckel's cartilage; *mx*, maxillary; *d*, dentary; *c*, coronary; *p*, palatine; *md*, mandibular.

ticular end of Meckel's cartilage, and there becomes made over into a middle-ear bone, the *incus*, which lies next the ear-drum. So it results that the articulation between the malleus and the incus in the middle-ear chamber of mammals corresponds exactly to the articulation between the upper and lower jaws of the dogfish. In the same way the upper end of the hyoid arch forms the third in the chain of middle-ear bones, the *stapes*.

Thus these tiniest individual bones of the skeleton, have had a checkered career which hardly has a parallel in any other part of the marvellously adapted human mechanism.

CHAPTER VIII

THE HUMAN SKULL

1. Protective Adaptations

When one takes a human skull in his hands and views it from all angles thoughtfully, as Hamlet viewed poor Yorick's skull, it invites contemplation. Only the uninitiated shudder and turn away. The moralist is reminded of the inevitable end of every human life; the artist sees in it a continuous complex of curving lines that spell grace and beauty; while the biologist realizes that he has before him the culmination of countless adaptations, the age-long grist of a tireless evolutionary mill. The protective adaptations particularly strike the biological eye.

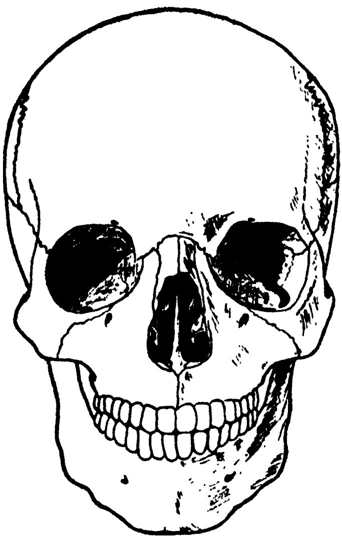


Fig. 99. — Face view of human skull. (After Spalteholz.)

The skull is first of all a dome (Fig. 99) which most effectively disposes of a minimum of material in a way mechanically fitted to resist pressure and strain. The

strength of the arch is there and chance blows are often robbed of their harmful results since the shape of the skull makes them glance off.

Moreover, the delicate sense-organs of the head are all placed in positions of the greatest possible safety compatible with the reception of external stimuli.

Thus the *sensory part of the ear* is buried deep in the temporal bone with a guarded passageway leading to it for the entrance of sound-waves. The *olfactory epithelium of the nose*, by means of which there is a sense of smell, is placed high up in the nasal chamber on the sides of the ethmoid bone and protected by the overhanging awning of the external nose. The *chemical sense of taste* is located well within the protective barrier of the jaws, while the *rotating eyeballs*, which like wonderful cameras that can not only photograph the tiniest object within touching distance but can also catch the picture of a twinkling star unthinkable millions of miles away, are surrounded by cave-like sockets of bone which expose little more than that part of the eye actually necessary to the reception of the light stimulus. Finally, any necessarily exposed or projecting parts of the skull, such as the external ears and the tip of the nose, are formed not of breakable bone but of bendable cartilage.

2. General Features

In describing the skull there are certain groups of features that may be spoken of first in a general way.

a. Cavities

The *cranial cavity*, occupied by the brain, is the most conspicuous cavity of the skull (Fig. 100). Its extent does

not set a limit to the size of the brain but rather the brain within determines the size of the skull. The size of the cranial cavity indicates in a general way the intelligence of the individual in question, but the fact that

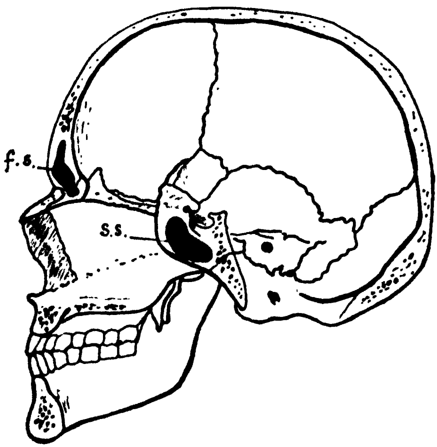


FIG. 100 — A median section of a human skull with the frontal (*f.s.*) and sphenoidal (*s.s.*) sinuses in black. (After Spalteholz.)

the average capacity of human males is greater than that of human females is no argument in favor of differential intelligence between the sexes. Of two dogs, belonging to the same species of *Canis familiaris*, the little one may be the more intelligent. It is quality not quantity that counts, consequently the size of the cranial cavity is not an infallible guide to brain efficiency.

Within the bones themselves there are certain definite cavities, moreover, which mark an increase in the size of

the skull without a corresponding increase in the size of the brain. These cavities are called *sinuses*. The *frontal sinus* (Figs. 100 and 120) in the frontal bone of the forehead over the eyebrows communicates with the nasal cavity behind so that a swimmer sometimes fills it unintentionally with water. To empty it he must throw back his head, poise on one foot and kick out vigorously with the other.

The *sphenoidal sinus* (Fig. 100) is a space within the complicated sphenoid bone around which the base of the skull is built, while the *antrum of Highmore* (Fig. 117) is a large sinus on either side of the nose above the eye-teeth in the maxillary bone.

Many smaller intercommunicating cavities are found in the skull as in other parts of the skeleton, causing the bones to be more or less spongy in character. An instance of such spongy bone is furnished by the *mastoid process* behind the ear, a section through which is shown in Figure 101.

The temporal bone on either side is hollowed out into an air-filled space that serves as the *middle-ear chamber*, containing the chain of tiny ear-bones which intensify the sound-waves while transmitting them to the innermost receptive part of the ear.

b. Fossæ

Partial cavities or depressions in bones are termed *fossæ*, from the Latin word meaning a "ditch." The most important of the fossæ found in the skull-bones are the following: the *orbital fossæ*, impressive, cone-shaped hollows which in man face front like binocular glasses but

in the majority of his vertebrate relatives open out laterally in two divergent directions (Fig. 99); the *nasal fossa*, likewise cavernous, holding a conspicuous position in the middle of the face and divided laterally into two symmetrical regions by the nasal septum; the *auditory fossæ*, blind alleys leading to the inner ear far within the temporal bones; the *temporal fossa* (Fig. 102), on either side behind the eye-sockets and above the cheek-bones forming a shallow depression in which lies the temporal muscle; and, finally, the *zygomatic fossa*, below the zygomatic arch or cheek-bone, continuous with the temporal fossa and partially occupied by the upward reaching ramus of the mandible or lower jaw.

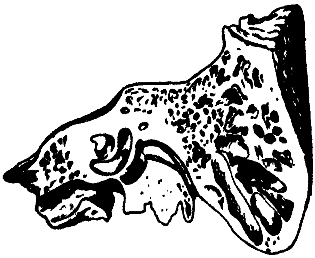


FIG. 101.—A section through the mastoid process, showing the spongy character of the bone.

c. Processes

The converse of fossæ are processes, or outgrowths. No part of the rounded bony skull projects obtrusively unless possibly the nasal bones. When extension is necessary it is accomplished not by outgrowths of bony tissue but by flexible cartilage which is less subject to injury, as for example, the end of the nose and the external megaphone part of the ears.

The most prominent processes on the skull are perhaps the *zygomatic arches* which are formed by the *malar bones* (Fig. 102) with contributory processes from the

maxillary and temporal bones. This complex stands out as a protective fender below the eye and across the cheek on either side and serves to shield the outstanding nose to a considerable extent from lateral blows.

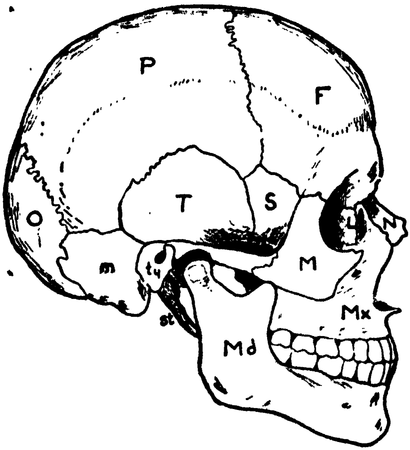


FIG. 102. — Side view of skull. *F*, frontal; *L*, lacrymal; *M*, malar; *m*, mastoid portion of the temporal; *Md*, mandible; *Mx*, maxilla; *N*, nasal; *O*, occipital; *P*, parietal; *S*, sphenoid; *st*, styloid process. (After Spalteholz.)

Other processes less exposed give surface for muscle attachment or mark the degenerate remains of former structures. Of these there may be mentioned the *mastoid process* of the temporal bone, rounding out on either side behind the ear; the *styloid process* (Figs. 102 and 96), a slender relic of the upper end of the embryonic hyoid arch, now fused to the temporal bone just between the mastoid process and the articulation of the lower jaw;

and the *pterygoid processes* (Fig. 103), which are safely buried at the base of the skull where they appear as sharp projections from the irregular sphenoid bone. They represent all that is left of the pair of pterygoid bones that, like some people, are noted not for what they are doing now or ever will do in the future, but for what their forebears have accomplished in the past.

d. Sutures

The bones of the skull fit together edge to edge by means of sutures, or joints that do not allow motion. Sutures usually appear upon the surface of the skull as irregular lines formed by the dovetailing together of the edges of the flat skull bones not only horizontally, but also vertically (Fig. 104). This results in interlocking joints which are almost as firm as solid bone. The curving suture between the squamosal and parietal bones on either side of the head above the ears, however, is not of the interlocking type but is squamous or scalelike, that is, one bone shingling over another.

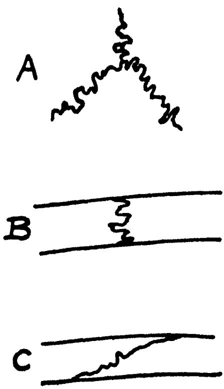


FIG. 104. Sutures. *A*, surface view; *B*, cross-section; *C*, cross-section of squamosal suture.

In general, sutures in the skulls of Europeans are more tortuous than are those of primitive peoples, such as Australians, while in old age they may disappear completely when the bones fuse together.

Fig. 103. — View of the base of the skull. (From an original drawing by George Hauman.)

The principal sutures of the skull serve as anatomical landmarks. Between the parietal bones, dividing the head into right and left halves, is the *sagittal suture* (Fig. 105). At right angles to this and separating the

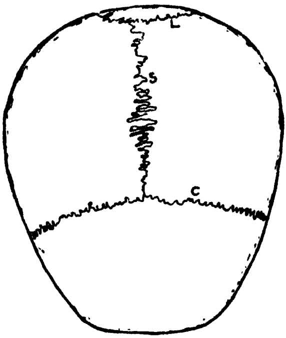


FIG. 105. — The top of the skull. *C, coronal suture; L, lambdoidal suture; S, sagittal suture.* (After Spalteholz.)

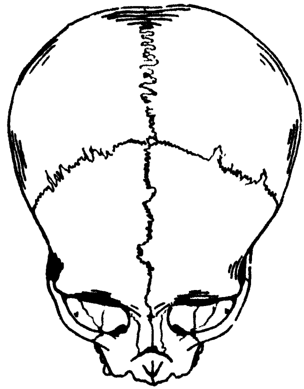


FIG. 106. — The skull of a young boy, showing the *metopic suture* separating the frontal bone into two parts. (R. S. S.)

parietal bones from the frontal is the *coronal suture* (Fig. 105). On either side like rainbows above the ears are the *squamosal sutures* (Fig. 102) already mentioned, while under the whirlpool of hair at the crown of the head, like an inverted wedge at the posterior end of the sagittal suture and separating the parietal bones from the occipital, is the *lambdoidal suture* (Fig. 105).

The frontal, or forehead bone is double in the human embryo and for some time after birth the two bones are separated by the *metopic suture* (Fig. 106). This sometimes persists in adults but in more than ninety per cent

it becomes entirely obliterated so that the frontals present the appearance of a single bone.

e. Fontanelles

When the skull bones develop, they grow out from centers of ossification like the spreading ripples from a pebble thrown into a quiet pond. The result is that when the advancing edges of three or more enlarging bones meet, a small uncovered area is temporarily caught between them where they come together. This is a *fontanelle*, so named by some imaginative father of anatomy because the throbbing of the blood-vessels of the human infant's brain, which is visible through these openings, suggested a "little fountain."

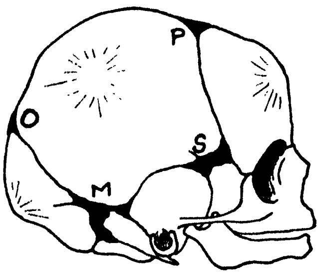


FIG. 107. — The skull of a new-born infant, showing the location of the fontanelles. *O*, occipital; *P*, parietal; *M* mastoid; *S*, sphenoid. (After Kollmann)

At least six fontanelles (Fig. 107) are present at birth in man, as follows: a large diamond-shaped *parietal fontanelle* on the top of the head between the frontal and the two parietal bones, which does not close until about the end of the second year; the *occipital fontanelle*, triangular in shape and lying between the occipital and the parietal bones, that closes at the end of a few months; the small paired *sphenoidal fontanelles* which are formed on either side of the skull by the union of the frontal,

parietal, temporal and sphenoid bones, and the *mastoid fontanelles*, likewise small and paired, that occupy the posterior space between the parietal, occipital and temporal bones.

These fontanelles are an adaptation no doubt of great practical value in childbirth. So long as they persist the separate bones of the skull can move upon each other with considerable freedom, even to the extent of temporarily shingling one over the other. Thus it is possible at birth, if the head has become misshapen in the process, to mold the skull without injury back into conventional contours almost as if it were clay. Certain primitive races like the Flathead Indians, for example, have seized upon this possibility of molding the newly born infant's plastic skull in order to acquire an abnormal shape of the head that, if not an improvement upon nature at least has the quality of lending distinction to its possessor.

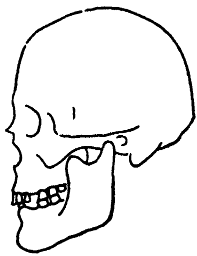


FIG. 108. — Unintentional occipital deformation due to cradle-board. Southwest U. S. Indian. Outline from photograph H/3670. Amer. Mus. of Nat. Hist.

Mr. Louis R. Sullivan, of the department of Ethnology in the American Museum of Natural History, kindly contributes the following information concerning head deformation in North America.

"The study of physical types in America is complicated by the widespread deformation of the head. In some cases it is unintentional, being produced by the hard pillows, and cradle-boards used (Fig. 108). In many instances, however, the head has been intentionally de-

formed by mechanical devices. The *two* principal types of artificial deformation are the fronto-occipital flattening (Fig. 109) and the Aymara conical distortion (Fig. 110).

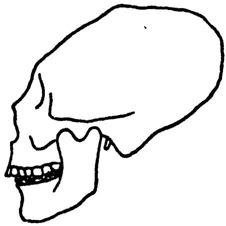


FIG. 109. — Fronto-occipital flattening of the skull of a Northwest coast Indian. Outline from photograph T/22177. Amer. Mus. of Nat. Hist.

"The unintentional flattening of the occiput occurs with greatest frequency among the Indian tribes of the Southwest. It has also been found pretty generally in the skeletal remains from mounds and graves throughout the greater part of the United States. It is a very common occurrence even among modern civilized peoples (some Scandinavians and people of Asia Minor).

"Intentional fronto-occipital flattening is found around two main centers, the Northwest coast and the Southeastern areas. It is usually produced by fastening a board to the head of the cradle-board by a hinge and placing a weight on the free end. This gives a lever of the second class working on the same principle as a nutcracker (although it never cracks the nut!). In the Southeastern area, similar results are produced by means of heavy sand-bags placed on the forehead thus compressing the occiput against the cradle-board. This type of deformation

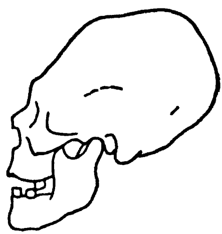


FIG. 110. — Aymara or conical deformation due to bandages. Peruvian Indian. Outline from photograph 99/3515. Am. Mus. of Nat. Hist.

is also found in South America, Malay peninsula, and Philippine Islands.

"The Aymara or conical distortion is found only among the Koskimo of Vancouver Island in North America, although it is the prevalent type of deformation in South America (Peru and Bolivia). Bandages are wrapped around the skull over the frontal and under the occipital regions. This produces a long, drawn-out, bug-like skull.

"There are various sub-types of each of these deformations. The custom was previously widespread, being recorded in one form or another from Africa, Malay, Philippines, France, Scandinavia, and Asia Minor. It is becoming less common in America at the present time.

"In some tribes the entire population practiced deformation while in others it was confined to one sex or even to the chiefs alone.

"Investigation has shown that it does not affect the mental ability of the subject and that it is not transmitted."

f. Foramina

Foramina are persistent holes that penetrate the walls of the skull, chiefly for the passage of nerves and blood-vessels. They frequently serve the comparative anatomist as landmarks for defining skull-bones after fusion has taken place, since their definite association with certain bones is quite constant throughout the vertebrate series.

The largest foramen of all is the ***magnum foramen*** (Fig. 103), through which the nerve-cord passes in becoming continuous with the brain. All together there

are upwards of one hundred foramina in the skull, most of which are distributed ventrally and laterally in the protected floor region rather than in the exposed dome above.

3. A Catalog of the Human Skull-bones

A catalog of the human skull-bones, with numerical differences in embryonic and adult life, together with a list of the bones with which each one comes in contact, is given in the following table:

THE HUMAN SKULL BONES

Group	*Name*	*Abbreviation*	*Articulates with*	NUMBER	
				Embryo	*Adult*
Cranial	Occipital	O.	Par. Par. T. T S. Atlas	5	1
	Parietal	Par	Par. O. F. T. S.	2	2
	Frontal	F.	Par. Par. S. E. N N. Mx. Mx L. L. Mal. Mal.	2	1
	Temporal	T.	O. Par. S. Mal. Mx. M.	12	2
	Malleus	Mall.	I.	2	2
	Incus	I.	Mall. St.	2	2
	Stapes	St.	I.	2	2
	Sphenoid	S.	F. Par. Par. T. T. O. E. Mal. Mal. Pal. Pal. V.	10	1
Facial	Ethmoid	E.	S. S. F. N. N. Mx. Mx. L. L. Pal. Pal. Tur. Tur. V.	5.5	1
	Inferior Turbinal	Tur.	E. Mx. Pal. L.	2	2
	Nasal	N.	F. E. Mx. N.	2	2
	Lacrymal	L.	F E. Mx. Tur.	2	2
	Vomer	V.	S E. Mx. Mx. Pa . Pal.	1	1
	Superior Maxillary	Mx.	F. E. N. Mal. E. Pal. Tur. V. Mx.	4	2
	Palatine	Pal.	S. E. Mx. Tur. V. Pal.	2	2
	Malar	Mal.	S. F. T. Mx.	2	2
	Mandible	M.	T.	6	1
	Hyoid	H.		5	1
				68	29

4. A Brief Description of the Skull-Bones

a. Occipital

The *occipital bone*, which is built around the magnum foramen, results from a fusion of four embryonic bones,

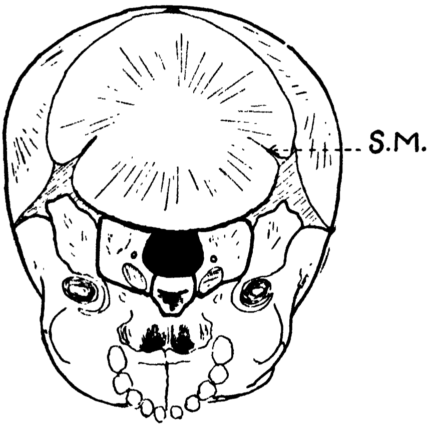


Fig. 111. — The base of an infant's skull before the fusion of the occipital bones. *S.M.*, the ***suture of Mendosa*** which tends to separate the supra-occipital into an upper "investing" and a lower "replacing" region.

the ***supra-occipital*** above, an ***ex-occipital*** on either side and the ***basi-occipital*** below (Fig. 111). This fusion normally occurs about the fifth year.

Externally the supra-occipital region bears transverse ridges known as the *external occipital crests* that during life may be felt under the skin at the back of the head. These ridges are of much greater prominence and importance in quadrupeds (Fig. 30) than in man because

they furnish attachment for the *ligamentum nuchæ*, a kind of anatomical guy-rope, as well as for the neck muscles both of which help to hold out the head in a horizontal position.

The inner surface of the supra-occipital region also possesses ridges that mark off shallow internal depressions in which there lie, somewhat separated from each other, the cerebellum and the cerebrum of the brain. When the occipital bone is held up between the eye and the light, it is seen to be of unequal thickness, much thinner where the shallow brain depressions are and thicker around the foramen magnum, across the ridges and along the sutural margins.

The supra-occipital bone is peculiar in that it has a double origin. Its lower half next to the magnum foramen, like the other occipital elements, is of cartilaginous "replacing" origin, while its squamous upper part, which fits in between the two parietals, is of the same embryonic origin as the parietals themselves, that is, it ossifies directly from membrane and is an "investing" bone belonging to the outer embryonic skull. The occasional presence of an imperfect suture, the *sutura Mendosa* (Fig. 111), between the two parts of the supra-occipital in question is further evidence of the dual nature of this part of the occipital bone. Moreover, the upper part of the supra-occipital is always a separate bone in certain mammals, the horse for instance, where it is termed the *interparietal bone*,

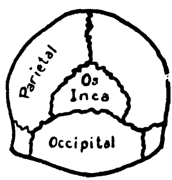


FIG. 112. Diagram of the back side of a skull showing the presence of the *Inca bone*. (After Wiedersheim.)

while occasionally it is independently present in man when it receives the name of the *Inca bone* (Fig. 112), because it has been frequently found in the skulls of the vanishing Peruvian aborigines or Incas.

At either side of the foramen magnum on the ex-occipital region is a prominence bearing an articular surface, the *occipital condyle* (Fig. 103), by means of which the skull moves upon the first cervical vertebra, or atlas.

The basi-occipital component of the occipital bone helps to form the floor of the skull.

b. Parietals

The *parietals* (Fig. 105), or wall-bones, are two bulging bones which constitute most of the vaulted roof of the cranial dome.

c. Frontal

The *frontal* bone (Fig. 99) is the part of the skull that gives shape to the forehead and helps to form the cavernous orbits in which the eyeballs are buried. From it project the horns of certain hoofed animals and even in man two radiating centers of ossification, which appear about the eighth fetal week, project prominently in reminiscent manner (Fig. 107) from the points where the horns of horned animals arise.

Embryologically the frontal bone is paired and as already noted, the two bones retain their individuality for some time after birth, separated clearly by the median metopic suture (Fig. 106) in line with the sagittal suture between the parietals.

When the thick *superciliary ridges* above the orbits are

excessively developed, the skull takes on an ape-like appearance. However, the development in this region of the frontal sinuses, which do not attain their fullest expression until after puberty, tends to minimize this simian character.

The double layer of bony tissue, resulting in the superciliary region of the forehead from the formation of the frontal sinuses as its outer and inner walls, furnishes a first and a second line of skeletal defence for the protection of the brain beneath.

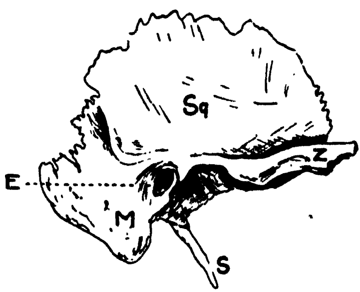


FIG. 113. — The right temporal bone as seen from the outside. *E*, external opening of ear; *M*, mastoid region; *S*, styloid process; *Sq*, squamosal region; *Z*, zygomatic process.

Above the nose and between the two superciliary ridges is a smooth depression called the *glabella* (Fig. 99), which furnishes a landmark of considerable importance in cranial measurement.

Between the two orbital areas of the frontal bone is a ragged arch, the *ethmoid notch*, which dovetails the frontal with the ethmoid and nasal bones, while on the concave surface on the inside of the frontal bone is a prominent ridge, the frontal crest, partially separating the two lobes of the cerebrum from each other.

d. Temporals

The *temporal bones* (Fig. 113) of the ear region are so called because white hairs, which are supposed to mark

the flight of time, usually appear first at the temples above the ears. They are perhaps the most complicated bones of the skull if their past history is taken into consideration, for within them is embedded the indrawn organs of hearing with their maze of passageways and chambers, the *accessory ear-bones* of roundabout splanch-

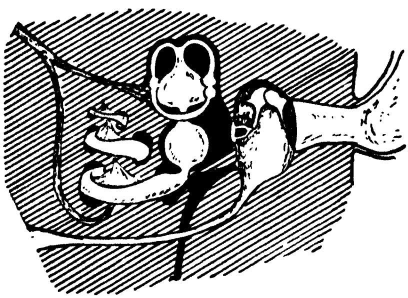


FIG. 114. — Diagram of the mammalian ear showing the position of the three ear-bones in the middle chamber. (Modified from Kingsley.)

nic derivation, and those tiny spirit-levels of equilibration, the *semicircular canals* (Fig. 114).

In some lower vertebrates the cartilaginous auditory capsule of the inner skull ossifies eventually into three bones that surround the inner ear. These are the *prootic* in front, the *epiotic* above and the *opisthotic* behind. In man these elements form a single bony envelope, the *petrosal* part of the temporal bone which encloses the chambers of the ear apparatus. It is somewhat pyramidal in shape and lies converging on either side along the lateral floor of the skull. The petrosal region is marked by a front door, the *external auditory canal*,

through which the sound-waves enter, and by a back door, the *internal auditory canal*, from which the short auditory nerve passes directly to the brain near-by. Within the petrosal bone and between these two doors is the middle-ear chamber across which stretches a chain of *three ear-bones* (Fig. 114); and a *bony labyrinth* which compactly encloses the sensory parts of the ear, namely, the *cochlea* and the *semicircular canals*. These latter stand at right angles to each other and have to do with the "sixth sense" of equilibrium so important to locomotor animals generally and to aviators in particular.

The projecting region of the petrosal bone extends forward and downward in the form of the cone-shaped *mastoid process* (Fig. 113) to which the digastric jaw-muscle and some other muscles find attachment, while inserted into a socket in the petrosal anterior to the mastoid region is the pointed *styloid process* (Fig. 102), projecting downward and forward. It is a remnant of the hyoid arch of the embryonic splanchnocranium.

A shieldlike investing bone of non-cartilaginous origin from the outer embryonic skull joins the petrosal complex and takes part in forming the lateral wall of the skull above. This is the *squamosal bone* which in man is particularly large because there is so much brain to cover. The squamosal and petrosal bones are still separate in many mammals throughout life and may remain unfused in man until after birth.

On the outside of the squamosal bone a process, called the *zygomatic process*, grows out like a flying buttress to meet the malar bone in the formation of the cheek-bone, while just beneath is a saucer-like socket, the *mandibular*

fossa, in which the lower jaw hinges on either side to the cranium.

Finally, in mammals, another embryonic bone from the non-cartilaginous outer skull, known as the *tympanic ring*, forms around the external auditory opening and fuses to the squamosal part of the temporal bone.

Thus each temporal bone, without reckoning the middle-ear bones which it surrounds, is made up of at least five embryonic elements of diverse origin.

c. The Middle-ear Bones

The three pairs of auditory ossicles, *malleus*, *incus* and *stapes* (Fig. 115), are the smallest individual bones of the body. They are circuitously derived, as previously pointed out, from the discarded remains of embryonic arches that help to make up the splanchnocranium (Fig. 96). They extend across the air-chamber of the middle-ear and transmit vibratory sound-waves that strike the ear-drum, which stretches across the external auditory passageway, to the *foramen ovale* of the inner ear in which the stapes fits like a piston. The plunging movement of the stapes in the foramen ovale agitates the lymph within the inner-ear which in turn stimulates the nerve-endings of the auditory sense-organ itself so that the impression of sound is sent along the auditory nerves to the auditory headquarters in the brain. The ear-bones articulating together as a system of levers act in such a

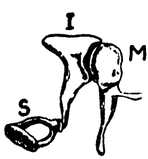


FIG. 115. The bones of the ear. *S*, stapes; *I*, incus; *M*, malleus. (After Henle, in Morris' *Anatomy*.)

way that the effectiveness of the vibratory stroke of the sound-waves is mechanically much increased.

f. The Sphenoid

The *sphenoid bone* forms the chassis-like foundation for the superstructure of the cranium. It is an extremely irregular bone made up of a body, two conspicuous pairs of wings and a pair of downward-pointing processes, the whole thing bearing a distant resemblance to a butterfly. Since it joins so many neighboring bones (see table, page 129), its outline in the adult skull is exceptionally fortuitous and somewhat difficult to trace. It may fuse at about the time of puberty with the occipital bone in the basi-occipital region.

Although the sphenoid appears as a single bone in the human adult, at least ten embryonic, or ancestral, bones take part in its formation, as follows: two median bones, the basisphenoid and the presphenoid,[1] arranged tandem fashion, form the "body" just anterior to the basioccipital region; two pairs of winglike bones extending laterally, respectively the orbitosphenoids in front which are attached to the presphenoid bone and form the "lesser wings," and the *alisphenoids* behind that arise from the basisphenoid and form the "greater wings"; and finally, the two *pterygoid processes* projecting downward from the junction of the body with the greater wings. Each pterygoid process is made up of two plates, a shorter, broader *lateral lamella* on the outside

[1] That these bones were ancestrally paired is indicated by the fact that each arises from two centers of ossification.

and a longer somewhat curved *median lamella* on the inside which terminates in the *hamular process.* All of the above-named sphenoid bones with the exception of the median lamella of the pterygoid processes are first mapped out in cartilage and consequently belong to the primitive inner embryonic skull.

FIG. 116. – The skull of a negro, showing the presence of the *epipteric* bone (*E*). (After Wiedersheim.)

There are in addition to the true sphenoid bones of the inner skull a pair of skeletal elements associated with them which do not have a cartilaginous origin and are consequently to be considered as parts of the outer embryonic skull. They are the *epipterics*, wedged in on either side between the temporal, parietal and frontal bones and the alisphenoid wing of the sphenoid in the region of the sphenoidal fontanelle. These bones, which are usually missing in the adult, are when present best seen before puberty. They are indicated in the case of a negro eunuch in Figure 116.

g. Ethmoid and Turbinals

The *ethmoid* is a delicate, spongy bone of triple origin that is placed between the orbits in front of the sphenoid. It shelters the organ of smell.

In the embryo the outer walls of the two cartilaginous capsules ossify, becoming the shell-like *ectoethmoids*, and between these two curving plates there forms a third vertical plate, the *mesethmoid.* Later all three of these embryonic elements unite to form the ethmoid which

straddles the nasal chamber as shown in diagrammatic section in Figure 117.

The mesethmoid forms a thin upward projection, the *crista galli*, at the point where it fuses with the ectoethmoid above, while below it forms a partition, the *perpendicular plate*, which divides the nasal chamber into right and left parts.

Projecting into the nasal chamber from the inner surface of each ectoethmoid are two delicate scrolls of bone, the *superior* and *middle turbinals*. A third lower pair, the *inferior turbinals*, are similarly placed with reference to the ectoethmoids but they are separate bones throughout life.

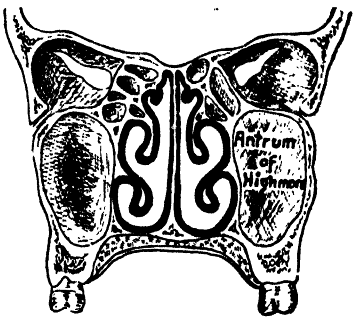


Fig. 117. — A vertical cut through the nasal region, showing the ethmoid and the turbinal bones (in black). (After Tillaux.)

On either side of the crista galli where the ectoethmoids join the mesethmoid horizontally is a bony area, the *cribriform plate*, which is perforated like the cover of a pepper-box for the passage of the brush-like olfactory nerves through to the small patches of sensory epithelium, situated within the nasal chamber above the superior turbinals.

In addition to the independent inferior turbinals just mentioned another pair of accessory bones is frequently associated with the ethmoid. These are two small, cone-shaped ossicles, the *sphenoidal turbinals*, that

form between the palatine, ethmoid and sphenoid bones and which usually fuse with the ethmoid about the fifth year.

h. Nasals

The *nasals* are two small bones that roof over the nostrils. They sometimes fuse together, more frequently, according to Wiedersheim, in Patagonians and South

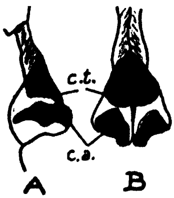


FIG. 118. — The flexible cartilaginous elements (in black) of the projecting part of the nose. *A*, side view; *B*, front view, *c. t.*, *cartilago triangularis*; *c. a.*, *cartilagines alaris*. (After Gegenbaur.)

FIG. 119. — "The external nose varies strikingly in the styles of its architecture." (After Gallup.)

African tribes than in other races. They always do so in the apes.

The bony bridge of the nose is extended and supplemented by three cartilages, the *cartilago triangularis* on the ridge and the paired *cartilagines alaris* at the sides of the nostrils, as shown in Figure 118.

One of the most dominant features of the face is the external nose which varies strikingly in the styles of its architecture (Fig. 119).

i. Lacrymals

These are a pair of small fragile fingernail-like bones placed in the front part of the inner orbital wall near the opening of the lacrymal foramen (Fig. 120) which allow surplus tears to run from the orbit down into the nasal cavity.

The lacrymals belong to the non-cartilaginous series of the outer embryonic skull and in man are degenerating structures, sometimes, in fact, being entirely absent. In certain mammals, however, they extend beyond the orbit and take part in the formation of the facial wall.

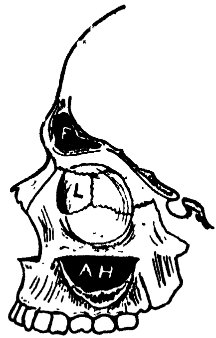


FIG. 120. — The upper jaw cut away to show the *antrum of Highmore* (*AH*). *F*, frontal sinus; *L*, lacrymal bone.

j. The Vomer

This thin "plowshare bone" is set up on edge between the sphenoid and the mesethmoid forming the lower posterior part of the nasal septum.

k. The Superior Maxillaries

The upper jaw on either side results from the fusion of the embryonic maxillary and premaxillary, which the poet Goethe, who was also a comparative anatomist of distinction, discovered in man. Both premaxillary and maxillary bear teeth.

The upper jaw consists of a main part of *body*, hollowed out by a large irregular sinus, the *antrum of Highmore* (Figs. 120 and 117), and of four outlying extensions, as

follows: the *nasal process*, that extends up to the nasal bone thus forming a part of the front wall of the face; the *malar process*, reaching out like a flying buttress to the malar bone, in this way helping to make up the "cheek-bone" or zygomatic arch; the horizontal *palatine process*, meeting its mate from the other side to form the anterior part of the hard palate in the roof of the mouth; and the *alveolar process*, bearing the sockets in which are implanted the teeth of the upper jaw.

l. The Palatines

The *palatines* (Fig. 103) are two bones hardly showing on the outside of the skull. They are considerably modified in man from their ancestral prominence as parts of the upper jaw of selachian fishes. Each is made up of a *perpendicular plate*, that articulates obscurely with various bones thus helping to form a part of the floor and outer wall of the nostrils, as well as a small part of the orbit, and a *horizontal part*, that joins to the palatine process of the superior maxillary, and with its fellow from the opposite side completes the posterior part of the hard palate.

m. The Malars

Between the zygomatic process of the temporal and the malar process of the superior maxillary, the *malar* bone (Fig. 102) extends completing the zygomatic arch or "cheek-bone."

n. The Mandible

The largest facial bone is the horseshoe-shaped *mandible* (Fig. 128) which is hinged to the squamosal part of

the temporals and hangs suspended below the other facial bones. It is a dense bone carrying a row of eight teeth on each side, set in sockets along the *alveolar border* (Fig. 42), and is generously equipped with strong muscles to serve in mastication.

The two halves of the lower jaw meet in front to form the chin, while at the opposite or hinge end each half extends upward as two processes, the *coronoid* in front and the *condylar* behind.

The embryonic forerunner of the mandible is Meckel's cartilage (Fig. 96) which is the lower half of the first, or mandibular arch of the splanchnocranium. Around this cartilaginous core various investing bones develop, notably a *dentary* bearing teeth and a *splenial*, on the inner side. Meanwhile Meckel's cartilage itself disappears except at the two ends. The proximal end forms the malleus of the middle ear while the distal end, the *mento-mandibular*, ossifies to form a part of the chin. The two mento-mandibulars fuse together about the end of the first year after birth.

Possibly other embryonic elements take part in the formation of the human lower jaw. It is surely true in the case of other vertebrates (see Fig. 97, of the alligator's jaw, Chapter VII), but the obliteration of embryonic details occurs very early in man, since ossification has already begun by the eighth week of fetal life.

o. *Hyoid*

The *hyoid complex* (Fig. 121), although it hangs suspended in the anterior part of the neck just above the "Adam's apple," where it may easily be felt by pinching

with the thumb and finger, is still embryonically to be reckoned as a part of the skull. It furnishes support for the tongue and has to do with the voice-box, or *larynx*. It is made up of a *body* and two curving processes, the *greater horns* and the *lesser horns*. Although held in place by ligaments and muscles, yet it has no articulation with any other bone.

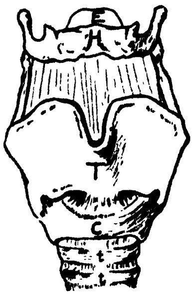


FIG. 121. — Front view of a human larynx. *H*, hyoid bone with lesser and greater horns; *E*, epiglottis; *T*, thyroid cartilage ("Adam's apple"); *C*, cricoid cartilage; *t*, *t*, tracheal rings of the windpipe. (After Cunningham.)

Embryologically the body is the basal part of the hyoid arch (second splanchnic). Other remains of this arch are represented in the *stapes* of the middle ear, the *styloid process* of the temporal bone, the *lesser horns* of the hyoid and, finally, the *stylo-hyoid ligament* which extends between these two last mentioned parts and by means of which the entire hyoid apparatus is hung to the cranium.

The greater horns are the persisting remnants of the first gill-arch (3rd splanchnic) while the Adam's apple, or the *thyroid cartilage* of the larynx, represents corresponding relics of the second and third gill-arches of the embryo.

CHAPTER IX

CHANGING FASHIONS IN SKULLS

1. Craniometry

While all skulls are referable to a common plan, as pointed out in the two preceding chapters, no two are exactly alike. Human skulls may vary in a general way with age, with sex, with race and individually. Even children of the same parents have differently shaped skulls. When human skulls are compared with those of anthropoid apes and other vertebrates, still more striking variations are apparent on the most casual observation.

In order to reduce these generalizations to more exact expression, various schemes of measurement have been devised from time to time upon which a science called *craniometry* has been built.

Only three of the many standards employed in craniometry will be mentioned as illustrative of the methods by means of which variations among skulls may be measured.

a. Camper's Angle

Camper's angle, named for a Dutch physician, Pieter Camper (1722–1789), was one of the first skull measurements employed. It gives the angle of the face and is determined by two straight lines, as shown in Figure 122, one from the external ear-opening to the base of the nasal fossa and the other from the central point of the

forehead (*glabella*) between the orbits to the anterior surface of the incisor teeth.

This standard is open to considerable error, because no one of the landmarks selected for measurement is an unmistakably fixed point, yet when applied to a series of skulls its diagnostic value in determining the evolutionary sequence is plainly apparent.

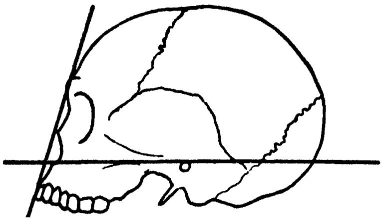


FIG. 122. — A profile of a skull, showing Camper's angle. (After Topinard.)

Camper, whose investigation was primarily for the guidance of artists, says, "The angle which the facial or characteristic line of the face makes, varies from 70 to 80 degrees in the human species. All above is resolved by the rules of art, all below bears resemblance to that of the apes. If I make the facial line lean forward, I have an antique head; if backward, the head of a negro. If I still more incline it, I have the head of an ape: and still more that of a dog and then that of an idiot" (Fig. 123).

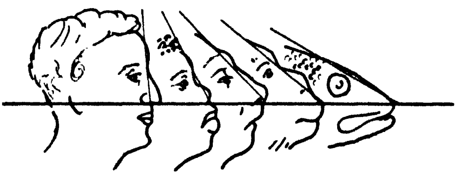


FIG. 123. – The evolution of the facial angle. (After Witkowski.)

Human varieties have been classified by means of Camper's angle into three groups: 1. *prognathous*, below 80 degrees, Tasmanians, Australians, Melanesians, Negroes; 2. *mesognathous*, from 80 to 84.9 degrees, Esquimaux, Chinese, ancient Egyptians, Japanese; 3. *orthognathous*, 85 degrees and above, Arabs, Europeans.

b. Cephalic Index

Another measure of skull variation is the cephalic index represented by the formula

$$\frac{\text{maximum breadth} \times 100}{\text{maximum length}} = \text{cephalic index}$$

By this means human skulls fall into three categories, as

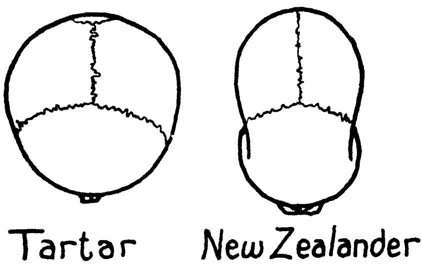


FIG. 124. – Extreme brachycephalic (Tartar) and dolichocephalic (New Zealander) skulls. (After Huxley.)

follows: 1. *dolichocephalic*, below 75%, Australians, Kaffirs, Zulus, Fijians, Esquimaux, Veddahs; 2. *mesaticephalic*, 75 to 80%, Swiss, Swedes, Scotch, Maori, American Indians; 3. *brachycephalic*, above 80%, Malays, Burmese, Lapps, Finns, Russians, Germans. Two extremes are represented in Figure 124, taken from

Huxley, that of a Tartar, 97.7%, and a New Zealander, 62.9%.

In the foregoing categories certain races of men have been cited as characteristically dolichocephalic, prognathous, etc. It should, however, be pointed out that such generalizations indicate only the prevailing type for the races in question, since upon exhaustive examination individuals are to be found within each race all the way between the extremes.

c. Cranial Capacity

The cubic contents of a skull may be measured by filling it through the magnum foramen with millet seed or buckshot after plugging with cotton whatever holes would allow leakage. The seed or shot may then be poured out into a graduated measure and the cranial capacity thus determined. By this method human skulls may be assigned to three groups: 1. ***microcephalic***, below 1350 cu. cm; 2. *mesocephalic*, between 1350 and 1450 cu. cm.; 3. *megacephalic*, above 1450 cu. cm.

2. Variations with Age

The relative size of cranium and face (see table on page 129) changes greatly during growth with a consequent modification in the appearance of the entire skull. In the human fetus the relation of the face to the cranium may be expressed perhaps as 1 to 8, while in the adult 1 to 2 would approximate the relationship.

The entire skull in the young fetus may be so disproportionately large as to equal the body in size (Fig. 125).

In the young child the face is small, typically round and quite overshadowed by the cranium. The nose, which at first is more of a promise than a realization, has the nostrils facing outward as in negroid races, rather

FIG. 125. — A human embryo at eight and one-half weeks, showing relatively large size of the head. (After Kollmann.)

FIG. 126. — The profile of infancy. (After Sir Chas. Bell.)

FIG. 127. — The profile of old age. (After Sir Chas. Bell.

than downward as in typical European stocks, while the chubby, muscular cheeks and protruding lips, which bespeak the sucking infant, still further emphasize the early insignificance of the nose (Fig. 126).

Later the jaws swell with erupting teeth, the chin protrudes and the nose gains its rightful prominence while the face assumes the adult oval contour. When the features of some interested relative are recognized in a

new-born babe, it is not because a truthful camera would record an actual likeness but because a subconscious comparative anatomist is hopefully viewing the subject with prophetic eyes.

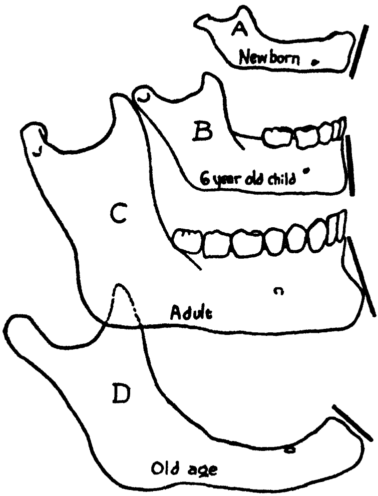


Fig. 128. — Changes in the chin angle during the life of the individual. (Ontogeny.) Compare with Fig. 129.

As old age approaches, the skull-bones become thinner and more fragile; the teeth forsake the jaws, and even the alveolar processes with the sockets that bore the teeth gradually become resorbed, so that the mouth region of the face is concave (Fig. 127) rather than convex as in the suckling babe. The nose, however, takes little part in the retrenchment of old age.

The relative age of an unknown skull may be approximately determined by the condition of the teeth and jaws, by the sinuses, which increase in size at puberty, and by the degree of closure of the sutures.

3. The Metamorphosis of the Chin

The chin is an excellent illustration of what is meant by the changing fashions of skulls.

In the infant, before the teeth have forced the lower

jaw to enlarge, the chin slopes backward (Fig. 128, A). Somewhat before puberty it has pushed forward until the angle it forms with the horizontal base of the jaw is not far from a right angle (Fig. 128, B). In adult life the chin projects outward (Fig. 128, C) and, last of all, in old age with the loss of the teeth and the resorption of the alveoli it projects still more at an acute angle (Fig. 128, D).

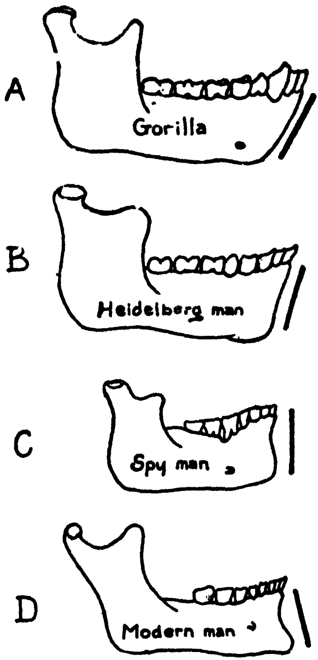


FIG. 129. — Changes in the chin-angle during the history of the race. (Phylogeny.) Compare with Fig. 128. (R. S. S.)

These successive changes which an individual passes through during a lifetime are strikingly paralleled in the evolutionary emergence of the human race, as shown in Figure 129. The chinless jaw of the gorilla appears in Figure 129, A, or, if one objects to the presence of an ape in the human ancestral tree, Fig. 129, B represents practically the same stage in the case of the famous *Heidelberg jaw* which is without doubt human and probably as ancient as any authentic fossil remains of mankind. This much studied fossil was found in 1907, buried near the mouth of the Neckar river valley, not far from Heidel-

berg, Germany, under conditions which unmistakably proclaim its great antiquity, for over it were seventy-nine feet of undisturbed strata (Fig. 130). The enormous superstructure of sand and sedimentary rock covering it

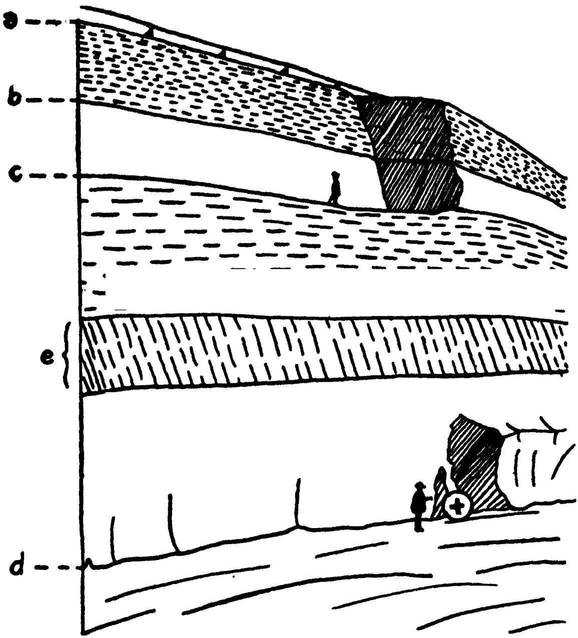


Fig. 130. — Diagram of the sandpit where the *Heidelberg jaw* was discovered. *a-b*, layer of "Newer Loess"; *b-c*, "Older Loess"; *c-d*, Mauer sands; *e*, a layer of clay. The cross indicates the spot under seventy-nine feet of undisturbed strata where the fossil jaw was found. (After Schoetensack, in Osborn's *Men of the Old Stone Age*. R. S. S.)

must have been originally slowly deposited over the dead remains of this interesting ancestor and subsequently, by the slow eroding action of the Neckar river in the formation of the Neckar valley, it must have as

gradually worn away until the bones were finally made accessible to an appreciative posterity.

Figure 129, C, outlines the chin of another well known human fossil, "*Spy I*" from Namur, in Belgium, which was found in 1886, and is also of very great antiquity although considerably more recent than the Heidelberg jaw.

Finally, Figure 129, D, presents an adult modern jaw for comparison.

We do not yet know what the typical jaw of the superman ages hence may be like, but we can safely guess that, whatever else may happen, the chin will not beat a retreat.

4. Sexual Differences

While it is by no means always possible, even for an expert ethnologist, to determine the sex of an individual from an examination of the skull alone, yet certain characteristics are, on the average, more pronounced in one sex than in the other.

The female skull tends to be smaller, lighter, lower, wider and shorter with respect to its base than the male skull. The face also is straighter, the orbits roomier, the mastoid processes and the occipital ridge less pronounced. In general the contours of the female skull are somewhat more infantile than are those of the male.

5. The Result of Uprightness

As the animal ancestors of man gradually shifted from either a quadrupedal or an arboreal to a bipedal attitude, certain accompanying modifications of the skull appeared.

In the first place not only the position of the magnum foramen but the plane of its orifice became changed as indicated in Figure 131. The plane of the nasal openings also changed from a direction facing anteriorly to one

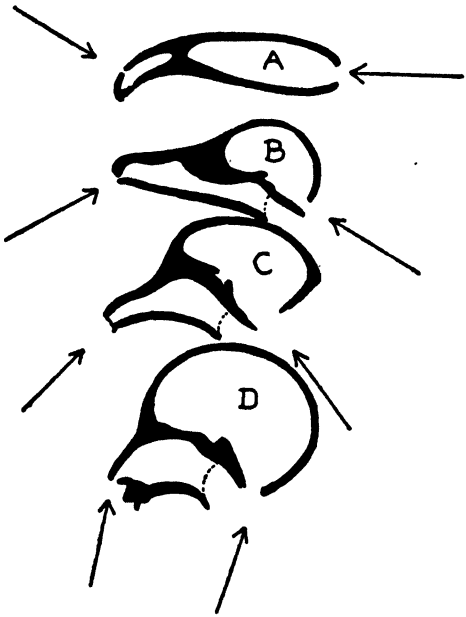


FIG. 131. — Sagittal diagrams through the skulls of a salamander (*A*), deer (*B*) baboon (*C*) and man (*D*). The arrows indicate an evolutionary change in the relation of the external nose-opening and the magnum foramen. (Modified from Wiedersheim.)

facing ventrally. It is as if the irresistible power of the growing brain resulted in pushing up the cranium, thereby bringing both the nasal openings and the magnum foramen into practically the same plane, just as the

ends of a glass tube change with relation to each other when the tube is bent.

A second modification of the skull that goes with uprightness of posture affects the outlook of the eyes, which are now brought into a position enabling them to sweep the horizon with much greater ease than is possible in the case of a quadruped whose projecting face tends to obstruct forward vision and to prevent the stereoscopic advantage of seeing the same object at the same time with both eyes. This point is made plain if one compares the skull of an animal like a hippopotamus (Fig. 132), with that of man. It is fatiguing for an ape to look the world straight in the face while it is anatomically easy for man to do so.

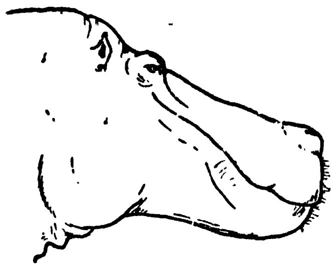


FIG. 132.—Head of a hippopotamus showing the projecting face. (After Hilzheimer.)

Obviously when the head is poised on top of the vertebral column instead of being held out horizontally, the occipital crests for the attachment of the sustaining ligaments and muscles become less necessary and are correspondingly reduced, just as, for the same reason, the neural spines of the cervical and thoracic vertebræ are prominent in a quadruped but are reduced in a biped.

Again, the upright posture brings the mastication plane of the teeth into a favorable horizontal position like that of millstones, as may be easily demonstrated

by closing the teeth upon a card. However, in the case of a quadruped like a cow the corresponding mastication plane slopes forward and downward making it necessary in the process of chewing to work partly against gravity (Fig. 133).

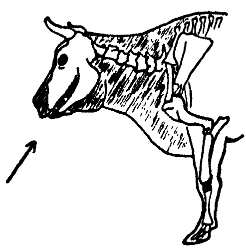


FIG. 133.—The mastication plane of a cow which makes it necessary to chew "up hill."

The more one regards the details of a human skull, with the idea of upright carriage in mind, the more does it appear to be a complex structure designed primarily for use in a position which it has inherited from its quadrupedal forebears, but which has now become changed to meet the new conditions imposed by an erect posture.

6. A Comparison of Man with Apes

Ever since Huxley's classical thesis on *Man's Place in Nature* appeared, the anthropoid apes have moved in good society.

There are four kinds of these sub-human caricatures, namely, gibbons, orang-outangs, chimpanzees and gorillas, which will always hold the lively interest of comparative anatomists and give uneasy concern to those humans who fear the security of their own aristocratic preëminence.

The embryo of the ape is much more human in all its details than the adult ape (Fig. 134), a significant fact that argues that the ape is a far-off cousin derived from common stock with man, rather than an ancestor of

man, as the partially informed have assumed was the humiliating but logical outcome of Darwin's theory.

By comparing a human skull with that of an ape the following characteristics of the latter appear: a more

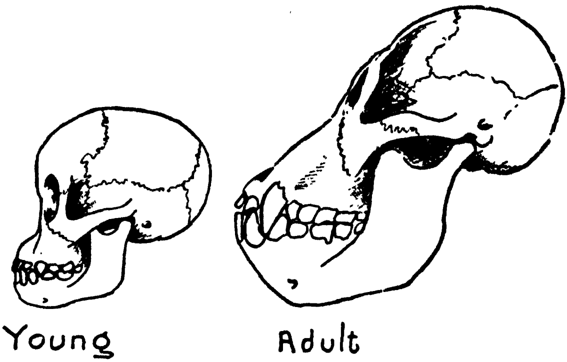


FIG. 134. Profiles of a young and an adult orang-outang showing that the young ape resembles the human more than when it is full grown. (After Wiedersheim.)

posteriorly placed magnum foramen; larger mastoid processes; a more massive jaw with more powerful teeth; a larger occipital crest and supra-orbital ridges; a smaller external nose but a more prognathous face; earlier closure of the cranial sutures; and a much smaller cranium.

This last characteristic is of the greatest importance because it forms the most nearly impassable gulf between apes and man. Topinard cites the cranal capacity of thirty-eight anthropoid apes as ranging from 387 to 623 cubic centimeters with an average of 475, while the average for a mesocephalic human may be placed at about 1400 cubic centimeters. The cranial capacity in the case of a female Veddah of the aboriginal stock of

Ceylon, which represents about the lowest normal human limit, is given as 1100 cubic centimeters. This is practically twice as large as that of the largest gorilla, the weight of whose body is easily twice that of a human being.

Man fortunately passes through a long fetal life, an extended infancy and a protracted childhood during which time the unfused bones of the skull allow the brain to enlarge. In apes, on the contrary, the limit of brain expansion is virtually set at birth and the cranial sutures are consequently already partly fused. Thereafter not the psychic cranium but the vegetative face-bones lead the way in development, and the anthropoid infant, which began life with so many hopeful human characteristics, grows up into a beast.

7. The Human Skull of the Future

The fashions of the human skull, which have perhaps shown more range and diversity than any other part of the skeleton, are still changing. What they may become ages hence is a matter of speculation. It is certain, however, that the teeth and all parts that have to do with the muscles of mastication are still degenerating. Moreover, the turbinal bones are growing smaller and all hall-marks of quadrupedal life are vanishing, while the cranium is probably increasing in size.

The psychic life, however, is rooted and grounded in the vegetative life, and there is a certain limit beyond which natural selection is unable to go. Consequently if we could call up before the eye of imagination our remote posterity, we should doubtless still find a func-

tional balance preserved between the cranial bones that house the intellectual life and the face-bones that minister primarily to the vegetative life. The indispensable need, therefore, of an apparatus of mastication insures its survival in the adaptive evolutionary rivalry of cranium and face-bones in the same way that the necessity of skeletal parts for the attachment of respiratory muscles is halting the progressive degeneration of the thoracic basket.

CHAPTER X

THE LOCOMOTOR SKELETON

1. The Necessity for Animal Locomotion

Attention has already been called in a general way to the necessity for locomotion among animals as contrasted with plants (see Chapter III).

The chemical elements common to all protoplasm, and therefore to the food of both animals and plants, are well-nigh universal in distribution in the form of carbon dioxide in the air, and of water, with various dissolved salts, in the soil (Fig. 135).

Meanwhile sunlight, the primal source of all energy possessed by organisms of every kind, shines alike upon plant and animal. The essential difference between plants and animals so far as locomotion is concerned, is that green plants by aid of the *chlorophyll* that makes them green are able to build up into organic foods, these inorganic compounds so universally distributed, thereby imprisoning the sun's energy. Since they can do this in a stationary position they do not need to move about for their daily bread. Most animals, on the contrary, without the Aladdin's lamp of chlorophyll, must seek their food directly or indirectly wherever plants have made it or perish. Hence the necessity for animal locomotion.

2. The Evolution of Locomotor Levers

As has already been said, the evolution of locomotor devices in the animal kingdom, shows that as soon as vertebrates emerged from water to land, legs became

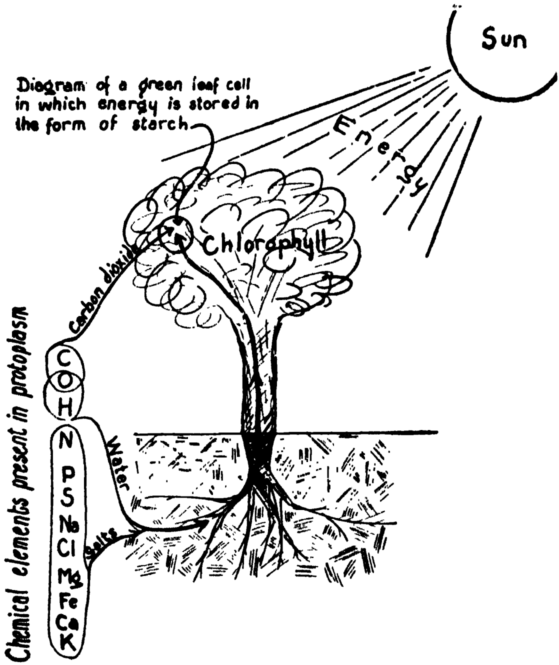


Fig. 135. — "The Aladdin's lamp of chlorophyll."

necessary to serve as supporting movable levers to propel them forward over the ground, since they could no longer swim fish-fashion by stroke of the tail.

The way in which these locomotor levers are now employed is the result of a special evolutionary process.

For example, in elongated animals like salamanders and alligators, there is little attempt to bear the weight of the

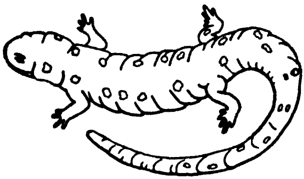


FIG. 136. — A salamander, showing weak lateral legs which push the body along without lifting it off the ground. (After Morse.)

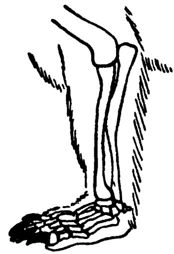


FIG. 137. — The plantigrade foot of a bear. (After Schmiel.)

body on the legs, which, extending as they do somewhat laterally as oars from a boat, are utilized principally to push the animal along while the weight of the body rests upon the ground (Fig. 136). It took time for the lateral legs of primitive land vertebrates to assume a vertical position and to evolve sufficient strength to raise the body off the ground.

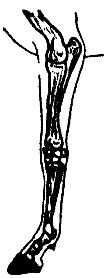


FIG. 138. — The unguligrade foot of a horse.

Since the time when the weight-bearing function of the legs became established, Nature has tried many experiments in locomotor levers, all the way from the sprawling plantigrade foot of the bear (Fig. 137) to that of the wonderfully specialized horse, which stands stilted on the tip of a single digit at the end of each leg (Fig. 138).

3. The Kinds of Appendages

Vertebrate appendages may be paired or unpaired. The latter sort are confined to water animals and are the more primitive, taking the form of *median fins* which are either continuous, as in *Amphioxus* and the lamprey eels, or broken up into separate dorsal, caudal and ventral fins. These, as well as the paired fins of fishes, are used not so much for locomotion as for balancing and steering.

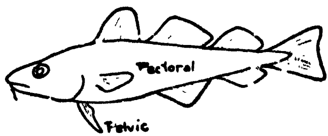


Fig. 130. — Outline of a codfish, the hind legs (pelvic fins) of which are in front of the front legs (pectoral fins).

In addition to median fins, fishes have two pairs of *paired fins*, namely, *pectoral* and *pelvic*, which are homologous to the locomotor appendages of the land vertebrates. Since they take no part in bearing the weight of the body they are not placed in such a way as to bear it as are the legs of the quadruped, but instead, may appear on the sides of the body at widely varying positions in different species. The pectoral appendages tend to shift backward with the formation of the neck while the pelvic appendages move forward.

This migration from the expected position is particularly true of the pelvic fins, so that in a case as extreme as that of the cod (*Gadus morrhua*) the pelvic fins are anterior even to the pectoral fins. In other words, the hind legs of a codfish are in front of its front legs! (Fig. 139.)

No vertebrate has more than two sets of paired appendages although several have only one, for example,

whales and sea-cows and that famous wingless New Zealand bird, *Apteryx*. A few, notably snakes, have not even a single pair.

4. Homology and Adaptation

Each vertebrate paired appendage is built on the same plan, that is to say, is made up of the same sequence of bones, which is represented diagrammatically in Figure 140.

This sequence, it will be noted, consists typically first of a tripod of bones, known as the *girdle*, by means of which it is anchored to the body, followed second by a large shaftlike bone, called *humerus* or *femur* according to its occurrence in the anterior or posterior pair of appendages. Next come two long bones, side by side, the *radius* and *ulna* respectively in the anterior appendage and the *tibia* and *fibula* in the posterior. Following these is a complex of several small bones which make up the *wrist* or *ankle*, and a set of five long slender bones, in the *palm* or *sole*. Finally, with one exception in the case of the thumb or big toe, where only two small bones terminate the series, there are at the tip of these long slender bones three more small bones placed end to end, known as *phalanges*.

Each bone of any appendage has its counterpart not only in the appendage on the opposite side but also in the appendage in front of or behind it as the case may be. The similarity from side to side is spoken of as *bilateral homology* while antero-posterior correspondence of parts is called *serial homology*. Not only may the homology between the bones that make up the locomotor append-

ages of a single individual be established *inter se* but the leg-bones of one vertebrate may be homologized with

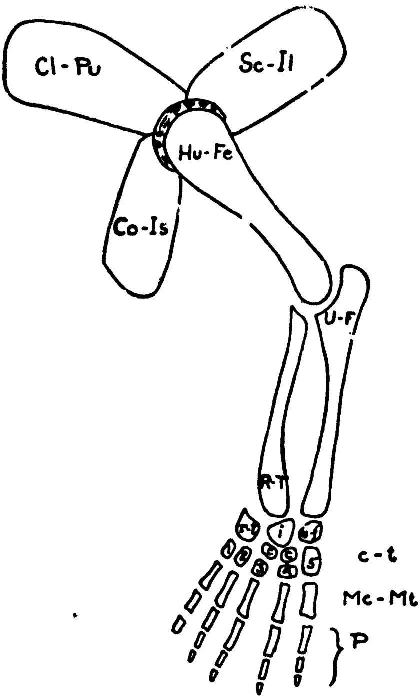


FIG. 140. — Diagram showing the homologies of vertebrate appendages. *Cl-Pu*, clavicle-pubis; *Sc-Il*, scapula-ilium; *Co-Is*, coracoid-ischium; *Hu-Fe*, humerus-femur; *U-F*, ulna-fibula; *R-T*, radius-tibia; *r-t*, radiale tibiale; *i*, intermediale; *u-f*, ulnare-fibulare; *c-c*, centrale; *1-5*, carpale-tarsale; *Mc-Mt*, metacarpale-metatarsale; *P*, phalanges.

those of an entirely different species of quite unlike external aspect. For example, each bone, in the flipper

of a whale or a seal, in the wing of a bat or a bird, or in the foreleg of a horse or a dog, has its homolog in the human arm.

The great diversity seen in vertebrate appendages that are all fundamentally alike, is associated with the wide range of function which vertebrate limbs perform. Climbing trees, burrowing in the ground, flying in the air, swimming in the water, jumping, running and grasping things each calls for a peculiar modification of the locomotor appendages.

5. The Girdles in General

As shown by comparative anatomy the girdles, or intermediary bones between the body and the limbs themselves, are each originally made up of three bones on either side of the body (Fig. 140). These bones meet at a common point like a tripod, and there the free limb articulates.

In the pectoral, or anterior girdle there is no articular connection with the main axial skeleton. The girdle is laced to the anterior part of the thoracic basket by means of muscles and ligaments, and while in man it may articulate with the front bone, or sternum, it never does so with the backbone. The pelvic, or posterior girdle, on the contrary, articulates with the backbone through the medium of the sacral "ribs" as shown in Figure 80, Chapter VI. This difference of girdle attachment gives a greater range of motion to the pectoral appendages and a firmer support to the pelvic appendages since the latter usually bear the weight of the body.

The three girdle-bones of each appendage occupy

homologous positions with respect to the girdle-bones of the other appendages. Thus one bone, either the *scapula* or the *ilium*, extends dorsally; another, the *procoracoid* or the *pubis*, is antero-ventral while the *coracoid* or the *ischium* is postero-ventral.

The articular cup for the front leg, at the junction of the three pectoral girdle-bones, is called the *glenoid cavity*, while the corresponding articular fossa on the pelvic girdle for the reception of the hind leg has been named the *acetabulum*, or "vinegar cup" by some imaginative anatomist of earlier days.

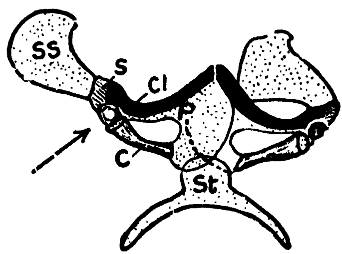


FIG. 141. — The pectoral girdle and sternum of a European toad, *Bombinator*, showing the clavicle (in black) taking the place of the procoracoid. *SS*, suprascapula; *S*, scapula; *Cl*, clavicle· *P*, procoracoid; *C*, coracoid; *St*, sternum. The arrow points to the glenoid cavity where the arm articulates. (After Wiedersheim.)

All of these girdle-bones are first modelled in cartilage which afterwards becomes replaced by bone. They therefore belong to the category of "replacing" bones similar to those of the inner skull. One "investing" bone, however, makes up a part of the pectoral girdle of the higher vertebrates including man. This is the clavicle, an antero-ventral bone without a cartilaginous ancestry, that has been substituted for the procoracoid. The fact that it is not a transformed procoracoid but a new bone of entirely different origin is proven by the condition in certain amphibians (Fig. 141) where the procoracoid and

clavicle are both present at the same time. In reptiles, particularly in some of the extinct fossil forms and in turtles, the triple character of the girdles is best seen. Among mammals, including man, still further evolutionary modifications have come about.

6. The Pectoral Girdle in Man

In man the pectoral girdle consists of two bones, the *scapula* and the *clavicle*, the one extending dorsally, the other articulating with the breast-bone in front.

On the scapula is the *coracoid process*, whose bony

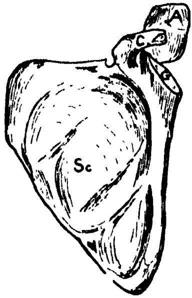


Fig. 142.—The left shoulder-blade as seen from the front. *A*, acromion; *C*, coracoid process; *G*, glenoid cavity for the articulation of the arm; *Sc*, scapula. (W. P.)

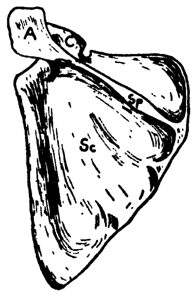


Fig. 143.—The left shoulder-blade as seen from behind. *A*, acromion; *C*, coracoid process; *Sp*, spina; *Sc*, scapula. (W. P.)

structure forms in separate centers of ossification from those of the scapula proper. This process is plainly a relic of the coracoid bone and its complete fusion with the scapula is delayed until about the age of puberty, a fact which still further indicates its independent origin.

The scapula itself (Figs. 142 and 143) has developed into a flat, thin triangular bone for the attachment of numerous muscles used in the movement of the arm. It is strengthened by increased thickness wherever stress comes along its margin and around the glenoid cavity; in addition a projecting ridge, the *spina scapulæ*, terminating in another conspicuous process, the *acromion*, further stiffens the scapula and increases the surface to which muscles may be attached.

The clavicle, or collar-bone, is a slightly bent bone extending outside of the thoracic basket from the acromion to the sternum (Fig. 59). It is the first bone of the entire body to ossify, beginning, in the case of man, about the fifth week of fetal life.

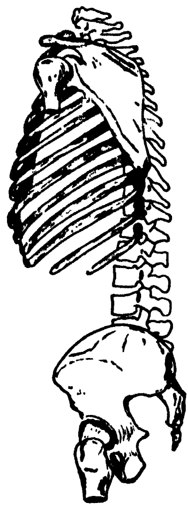


FIG. 144. — Skeleton of the trunk, showing the relation of the girdles to the vertebral column and to the appendages. (After Sobotta and McMurrich.)

7. THE HUMAN PELVIC GIRDLE

The human pelvic girdle (Fig. 144), like the pectoral girdle, is ancestrally composed of three pairs of bones, the *ilium*, *ischium* and *pubis*. Its triple composition is likewise apparent embryologically for it is not until about the time of puberty that the three elements on each side become completely fused into one element, known from that time on as the *innominate bone* (Fig. 145). The two innominate bones articulate with the sacrum behind in

an immovable joint, and in front with each other at the *symphysis pubis.* Together with the sacrum and coccyx of the vertebral column the innominate bones form the *pelvis*, a firm bony bowl attached immovably to the vertebral axis. On the outside of this pelvic ring are articulated the locomotor legs (Fig. 12).

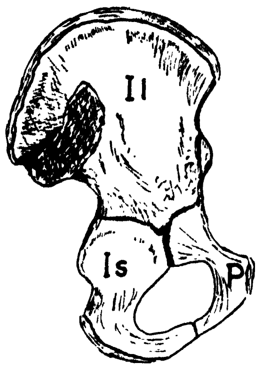


FIG. 145.—Inner surface of the innominate bone of a child of eight years, showing the component parts. *Il*, ilium; *Is*, ischium; *P*, pubis. (After Morris.)

The iliac portion of the innominate bone is broad and thin, expanding dorsally and laterally to form the protective and supportive pelvic basin in which lie a considerable part of the viscera of the body-cavity. The spread of the iliac bones is greater in the higher races than it is among primitive peoples, but in quadrupeds, where the weight of the viscera does not come so directly upon the pelvis, the iliac bones are narrower and less extended.

Furthermore, in quadrupeds the pelvic rim slants backward with its plane almost in line with the backbone (Fig. 31) so that it takes little part in the support of the viscera. With the assumption of the upright position, however, not only do the iliac wings broaden and spread out to form a supportive basin but the pubis projects forward making the angle formed by the plane of the pelvic opening and the dorsal axis approach a right

angle. The result is that the pelvis in front comes to bear some of the visceral weight.

As already pointed out, the curving heads of the two femurs together with the innominate bones of the pelvis

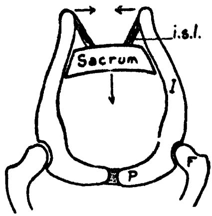


FIG. 146. — Diagram showing the sacrum as a keystone which, although upside down, nevertheless functions as such by reason of the action of the ileo-sacral ligaments, since the greater the weight from above, the more the iliac bones tend to pinch together thus holding the sacrum in place. *I*, ilium; *P*, pubis; *F*, femur; *i.s.l.*, ileo-sacral ligament. (Modified from Meyer.)

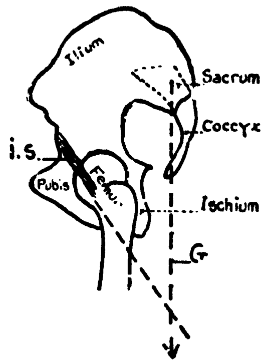


FIG. 147. — Diagram to show how the ileo-sacral ligament (*i.s.*) tends to prevent the body from tipping backward although the center of gravity (*G*) normally falls behind the femur. (After Meyer.)

form part of an arch which is completed above by the sacrum as a keystone (Fig. 12, Chap. II). On this arch the weight of the body is supported. The sacrum itself in this arch resembles a wedge wrong side up rather than an orthodox keystone. The faults of this mechanical curiosity, as pointed out by Meyer, are corrected by means of *ileo-sacral ligaments* that extend from the sacrum to the upper edge of the ilium (Fig. 146). When the weight of the body presses down upon the sacrum it pulls upon these ligaments with the result that the iliac

bones pinch together like a vise, thus holding the upside-down keystone firmly in its place. The greater the weight, the more firmly the sacrum is held.

Another ligament important in maintaining the upright posture of the body is the *ileo-femoral ligament*

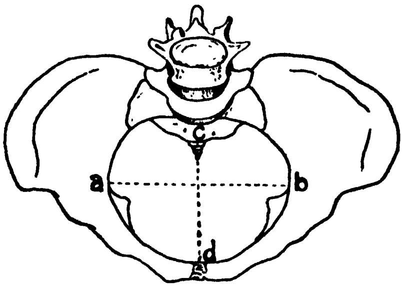


Fig. 148. — Outline of a female pelvis. (After Cunningham.)

which extends from the head of the femur on either side to the antero-ventral edge of the ilium. The center of gravity of the body falls through the sacrum, somewhat behind the attachment of the legs, to the pelvic girdle. A guy-line in the form of the ileo-femoral ligament acts as a counterbalance (Fig. 147) to prevent the body from falling over backward. The upright attitude is maintained obviously not by mechanical devices alone but by balanced muscular action, as shown by the collapse of an intoxicated person who has temporarily lost control of his muscles.

Various visceral tubes, the large intestine, the ureters and the reproductive ducts, converge into the pelvic ring. Out through this bony halo must pass every child that is born into the world. In consequence of the neces-

sities of childbirth, which involve not only bearing the weight of the pregnant uterus but also providing sufficient space for the emergence of the fetus, there is considerable difference between the male and the female pelvis. These differences begin to be apparent even in the fetus before birth.

Contrasted with those of the male the innominate bones of the female are seen to be thinner and smoother, the iliacs to spread less, and the ischial processes upon which the body rests when in a sitting posture to spread more. Furthermore, the entrance to the pelvis is more oval and the entire pelvic basin is shallower and broader than in the male. "The female pelvis has been well described as a short segment of a long cone as contrasted with the male pelvis, which is a long segment of a short cone." (Arthur Thompson.)

A comparison between the two sexes of the average dimensions in the entrance to the pelvis, is shown below, based upon data given by Rauber, referring to Figure 148.

	a to b	c to d
♂	12.7 cm.	11.2 cm.
♀	14.5 cm.	12.7 cm.

8. The Free Appendages

The homologies already mentioned between the free appendages are indicated more completely in the following table, in which the synonyms of the names employed for the various parts are included.

THE HOMOLOGIES OF THE FREE APPENDAGES

Pectoral			Pelvic		
Common Name	*Terms used in Human Anatomy*	*Terms used in Comparative Anatomy*	*Terms used in Comparative Anatomy*	*Terms used in Human Anatomy*	*Common Name*
Shoulder	Scapula	Scapula*	Ilium	Innominate Bone	Hip
		Procoracoid	Pubis		
	Clavicle	Clavicle			
	Coracoid Process	Coracoid	Ischium		
Upper Arm	Humerus	Humerus	Femur	Femur	Thigh
Fore-arm	Ulna	Ulna	Fibula	Fibula	Shank
	Radius	Radius	Tibia	Tibia	
Wrist	Scaphoid (Naviculare)	Radiale	Tibiale	Talus (Astragalus)	Ankle
	Lunatum (Semi-lunar)	Intermediale	Intermediale		
	Triquetrum (Cuneiform)	Ulnare	Fibulare	Calcaneus	
		Centrale I Centrale II	Centrale I Centrale II	Naviculare	
	Trapezium (Multiangular major)	Carpale I	Tarsale I	Cuneiform I (Ento-cuneiform)	
	Trapezoid (Multiangular minor)	Carpale II	Tarsale II	Cuneiform II (Meso-cuneiform)	
	Magnum (Capitatum)	Carpale III	Tarsale III	Cuneiform III (Ecto-cuneiform)	
	Unciform (Hamatum)	Carpale IV Carpale V	Tarsale IV Tarsale V	Cuboid	
Palm	Metacarpal I " II " III " IV " V	Metacarpale I " II " III " IV " V	Metatarsale I " II " III " IV " V	Metatarsal I " II " III " IV " V	Instep (Sole)
Fingers	5 Phalanges 5 " 4 "	1st Row 2nd " 3rd "	5 Phalanges 5 " 4 "	1st Row 2nd " 3rd "	Toes

The relative length of the arms and the legs varies with age (Fig. 149). Eventually the legs, which at first are shorter than the arms, come to be longer so that it is not easy for man to assume the quadrupedal position. Such a

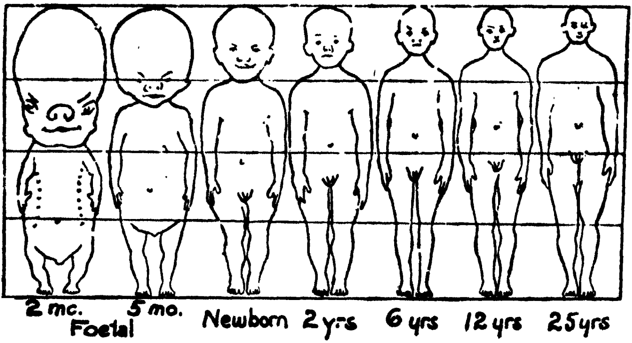


FIG. 149. — Figures illustrating changes in proportion during prenatal and postnatal growth. (After Stratz, in Morris' *Anatomy*.)

change of relation during development is similar to the change in the evolutionary series, diagrammatically represented in Figure 150.

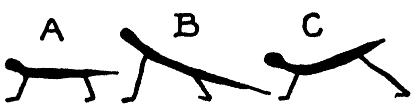


FIG. 150. — Diagrams showing the relation of the appendages in (*A*) a new-born child, (*B*) an adult ape and (*C*) an adult man. (After Wiedersheim.)

The first part of the budding appendage that shows on the side of a human embryo turns out to be the hand or foot (Fig. 151). This bud soon becomes scalloped, marking the future toes and fingers, and then,

after a "web-footed" stage, the separate digits are finally established. Meanwhile the long bones of the

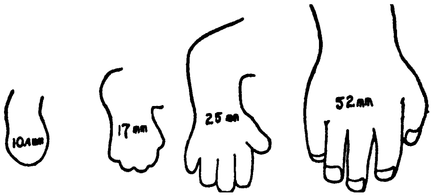


FIG. 151. — Successive stages in the development of the human hand. The figures indicate the size of the embryo in each case. (After Retzius.)

leg or arm push out the foot or hand, as the case may be, just as if these extremities were borne upon the end of an extending lever-like handle.

9. THE ARM

The human arm is a foreleg which has been emancipated from the work of locomotion and support. The inherited system of levers and joints which makes up the arm, has been diverted to various other uses, however, with conspicuous success. The function of the prehension of food, for instance, is no longer confined to the mouth and lips, as in many animals whose arms are still legs, nor are defensive out-riggers, like horns, any longer necessary, because the swinging arms take the place of such organs of defence.

The entire arm is pivoted to the pectoral girdle by a ball-and-socket joint which allows great freedom of motion, while other joints between the separate arm-bones limit the range of motion in each instance although

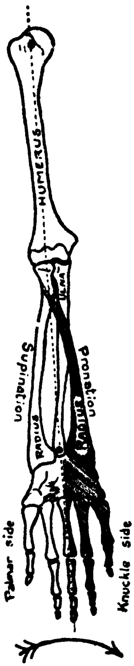


FIG. 152. — Diagram showing the relative positions of the radius and ulna in pronation and in supination. (After Heitzmann.)

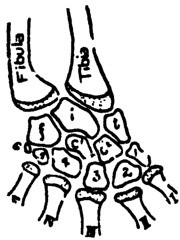


FIG. 153. — Tarsus of a salamander, *Cryptobranchus japonicus*. *f*, fibulare; *i*, intermediale; *t*, tibiale; c^1 and c^2, centralia; *1-6*, distal row of tarsals; *I-V*, metatarsals. (After Wiedersheim.)

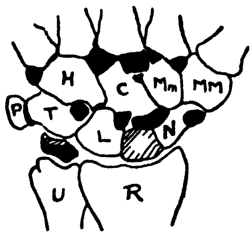


FIG. 154. — The volar aspect of a human wrist showing (in black) where extra wrist-bones have been found in various individuals. For the names of the wrist-bones see Fig. 156. (After Pfitzner.)

gaining in strength and effectiveness. Thus at the elbow there is a hinge-joint that moves in only one plane but which is rendered by this specialization all the more efficient.

The joints of the wrist and hand are mostly hinge joints moving likewise in one plane, but the rotation of the radius around the ulna (Fig. 152) brings the hinge action of the hand into any desired plane.

FIG. 155. The principal landmarks of the locomotor skeleton. (Modified from Hanke.)

Between the two rows of wrist-bones, that are invariably present in many animals including most monkeys and some apes, there are to be found one or more *central bones* (Fig. 153). For a long time these were not known in man. In 1874 they were discovered in the human embryo by Rosenberg. Their disappearance during the third fetal month is due to fusion with the radiale or naviculare (see table on page 174).

The fact that a careful and extended study of a large series of human wrist-bones, such as has been made by Pfitzner, reveals the presence in various situations of a great number of supernumerary wrist-bones, shows that this region of the arm is still being extensively molded by evolutionary factors. Figure 154 is a composite diagram after Pfitzner showing the location of fifteen extra bones found in different human wrists.

10. The Leg

Since the time when the arms were relieved from the work of locomotion and support in the evolution of man, the entire responsibility of these functions has been thrown upon the legs.

The *femur*, which is the largest bone in the body, is a strong pillar-like shaft, enlarged at either end for the attachment of muscles and articulation.

The *knee-joint*, like the elbow-joint, is a hinge, bending, however, in a direction opposite to that of the elbow-joint.

Between knee and ankle the *tibia* in man has monopolized the function of bearing the weight of the body, for the *fibula*, a degenerating bone so far as the supportive function is concerned, no longer articulates with the femur. Its value however, as an available surface for the attachment of muscles particularly useful to the evolving foot, insures its probable preservation from the anatomical scrap-heap. The tibia varies greatly in length in different races and even in different individuals of the same race. According to Wiedersheim it is the most variable bone in the entire human skeleton.

At the knee-joint there is an extra bone, called the *patella*, or knee-cap, which has no homolog at the elbow-joint. It is a "sesamoid" bone which, unlike other bones, is formed as a calcareous deposit in ligamentous tissue when subjected to continuous pressure.

The foot and its homolog the hand, with the ankle- and wrist-bones, complete the locomotor skeleton and will be considered in the final chapter (Fig. 155).

CHAPTER XI

THE HANDY HAND AND THE MAKESHIFT FOOT

1. The Parts of a Human Hand

The hand is made up of the wrist, the palm-bones, four fingers and a thumb.

The *wrist-bones* are arranged in two irregular rows each of which is composed of four bones. Beginning at the ulnar side three of the proximal row, the *triquetrum*, *lunatum* and *scaphoid*, articulate with the forearm, making the wrist-joint. The other bone of this row, the *pisiform*, does not touch the forearm but is joined to the triquetrum where it may be felt through the skin at the base of the palm on the little finger side. Each of the distal row of wrist-bones, known respectively as the *unciform*, *magnum*, *trapezoid* and *trapezium*, articulates distally with a metacarpal, or palm-bone, with the exception of the unciform which articulates with two metacarpals (Fig. 156).

All of these small wrist-bones are irregular, many-sided structures held together by ligaments and so playing upon each other as to allow considerable motion. They fit together as a whole forming a shallow trough with its concavity on the palmar side of the hand. Across this cavity stretches from side to side the *ligamentum carpi transversum* and under the bridge thus formed go in safety the tendons, blood-vessels and nerves that supply the fingers.

FIG. 156 — The right wrist and neighboring bones from the volar surface, separated from each other in transverse rows. *R*, radius; *U*, ulna; *N*, naviculare; *L*, lunatum; *T*, triquetrum; *P*, pisiforme; *MM*, multiangular major; *Mm*, multiangular minor; *C*, capitatum; *H*, hamatum; *I-V*,,metacarpals. (After Sobotta and McMurrich.)

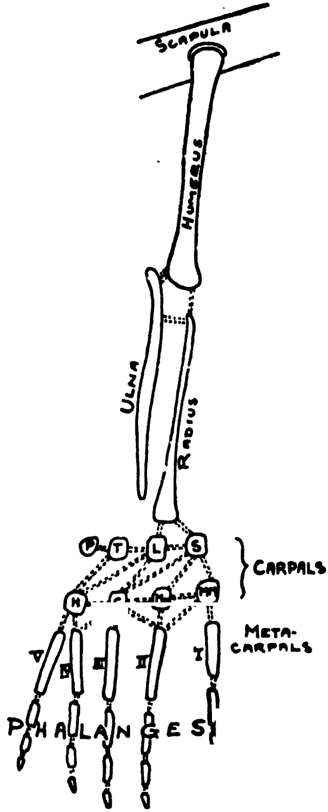


FIG. 157. — A diagram showing how the hand is hung upon the radius, and the articulations (dotted lines) of the wrist. For the names of the carpals, see text.

The articulations of the wrist-bones, as well as the other bones of the arm, are shown diagrammatically by the dotted lines in Figure 157. It will be seen from Figure

157 that the entire hand is hung principally upon the radius which is enlarged at the carpal end to receive it. Although the radius takes some part in the articulation of the forearm to the humerus at the elbow-joint, this function is mainly accomplished by the ulna which consequently is enlarged at this end. Such an arrangement makes it possible for the distal end of the radius, bearing the hand, to rotate freely in a half circle and to carry the complex of hand-bones with it.

When the radius and ulna are parallel the hands are palms up in an attitude of supplication. This is called *supination*. The opposite attitude of *pronation* occurs when the radius and ulna are crossed and the palm of the hand is turned down (Fig. 152, Chap. X).

The five palm-bones, *metacarpals*, are the long bones of the hand, each one of which is enlarged at either end and all of which are slightly divergent with relation to each other. The first metacarpal bears the thumb and is the shortest and stoutest, while the one supporting the index-finger is the longest.

A finger is made up of three bones, called *phalanges*, while the thumb has only two bones present. The longest phalanx is the proximal element of the middle finger which projects when the fist is clenched. The three phalanges of each finger, together with the opposability of the thumb, provide for the grasping function of the hand which would not be possible if each finger consisted of a single bone.

Five small *sesamoid* bones, embedded in tendon, are regularly present on the palmar side of the hand. One is at the interphalangeal joint, and two at the metacarpo-

phalangeal joint of the thumb while one each is at the metacarpo-phalangeal joint of the index and of the little finger. Frequently still other sesamoid nodules are found at the finger-joints.

2. Unusual Human Hands

Aside from the frequent occurrence of extra wrist-bones (Fig. 154, Chap. X), anatomical literature is full of

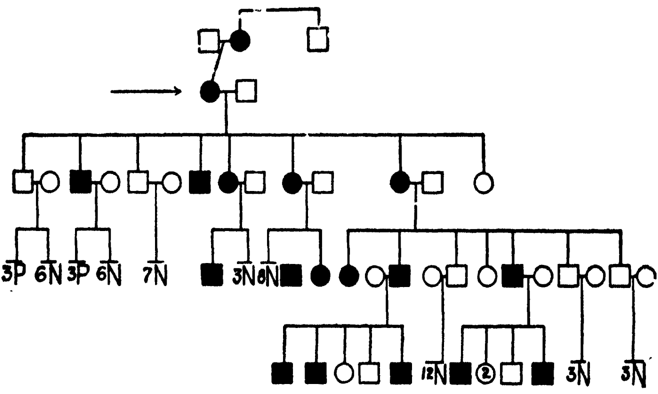


Fig. 158.—A pedigree of polydactylism. Affected persons are represented by black symbols. Squares represent males and circles, females. The letters *N* and *P* refer to normal and polydactylous individuals respectively whose sex was not learned. (From Lucas, in Davenport's *Heredity in Relation to Eugenics*.)

instances of abnormal hands, some of which are known to reappear in different members of the same family.

Davenport [1] cites the case of a polydactylous, or extra-fingered woman who had a polydactylous mother, and five of whose seven children were polydactylous. Six of her grandchildren also and five great-grandchildren were known to be polydactylous (Fig. 158).

[1] *Heredity in Relation to Eugenics*, p. 175.

Syndactylism, or growing of fingers together, is not unknown in man, and *brachydactylism*, in which one phalanx of each digit is missing, is occasionally seen. The latter furnished one of the first clear-cut cases (Farrabee, 1905) of a human peculiarity that was definitely shown to follow "Mendel's Law" of alternate inheritance. Figure 159 is a radiograph of a *polydactylous* hand of which one thumb is at the same time apparently brachydactylous but which in reality shows a fusion of phalanges rather than the loss of a phalanx. Bateson, in "Materials for the Study of Variation" (page 324) cites a long list of cases in man of polydactylism, syndactylism and brachydactylism as well as the reduction of the number of digits.

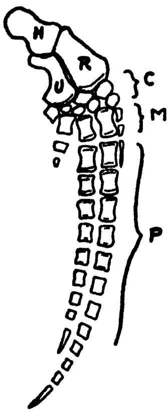


FIG. 160. — The flipper (arm) of a dolphin showing the separate bones which are homologous to those of a human arm. *H*, humerus; *R*, radius; *U*, ulna; *C*, carpals; *M*, metacarpals; *P*, phalanges. (After Flower.)

3. HANDS NOT HUMAN

The comparative anatomy of the hand is an alluring and illuminating field of study that must at least be mentioned in this connection, for evolution has worked out a great variety of problems in connection with adaptations of the hand.

In water dwellers like whales (Fig. 160) and seals, as well as the fossil ichthyosaurs and plesiosaurs, the hand became a flipper by the multiplication of phalanges and an inclusion of the whole flattened complex of bones

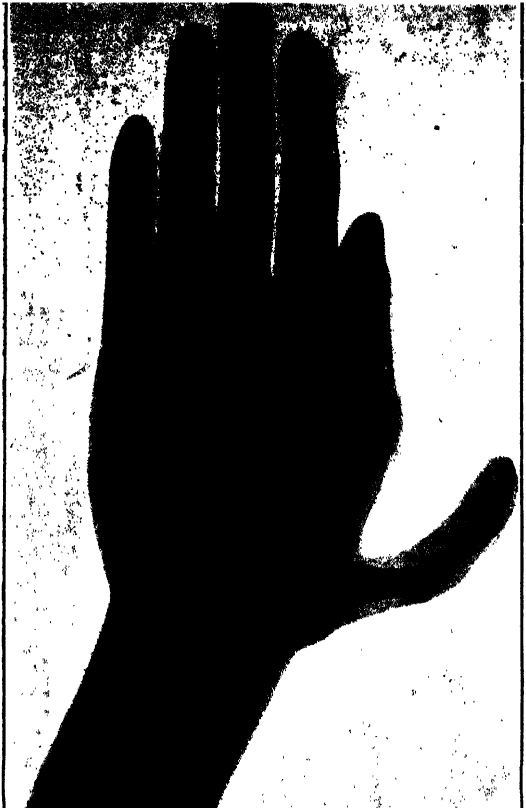


FIG. 159. — Radiograph of a polydactylous hand. The fusion of the two joints in the outer thumb suggest a brachydactylous condition. Negative No. 7642 '17. Rhode Island Hospital.

within a common skin. Among the ungulates, or hoofed animals, where the hand is specialized for support, there has been a progressive reduction in the number of bones

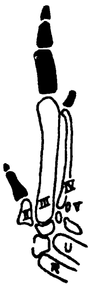


FIG. 161. — Diagram of the wing-bones of an embryo tern showing traces of three fingers (in black). (After Leighton.)

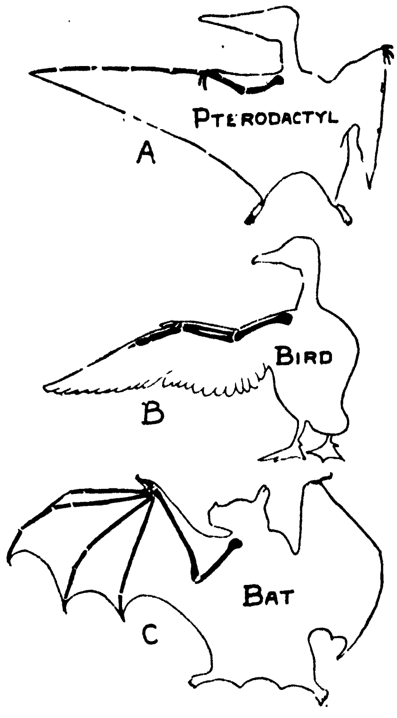


FIG. 162. — Three methods of flying with homologous appendages. (Modified from Pander and d'Alton.)

until, in the extreme case of the modern horse (Fig. 138), the third finger is the only one that remains.

The problem of flight has been solved in three ways by the hand. Among birds digits have been reduced to one,

although three still remain in the fossil *Archeopteryx* and in the embryo tern (Fig. 161). This single digit makes a firm axis to which are attached the light, air-resisting wing-feathers (Fig. 162, B). In bats the phalanges, except those of the thumb, are enormously elongated to

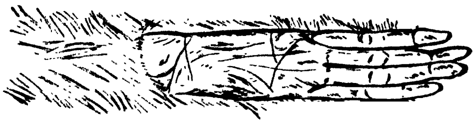


FIG. 163. — Thumbless hand of a spider monkey, *Ateles*. (After Haacke.)

support the thin web-like skin of the wings (Fig. 162,C), while in the extinct *Pterodactyls* the little finger was excessively developed to serve as a mast to carry the sail-like skin (Fig. 162,A).

Among the primates who begin to grasp things is found the hand that most resembles that of man. The winning feature that culminates in the human hand seems to be the opposable thumb. This is absent in most monkeys (Fig. 163) and is so poorly developed in the apes that it is rather ineffective as a grasping organ.

4. THE OPPOSABLE THUMB

The human hand takes part with the large brain in placing man triumphant at the head of animal creation. Without its aid the arts and sciences, which are the expression of human civilization, would not have been possible.

The hand is first of all a grasping organ on a movable handle that can hold a tool or grip a weapon (Fig. 164).

Without artificial aids of this kind man would still be a beast, for the only weapons and tools that a beast has, such as the goring horns of a bull or the chiseling teeth of a beaver, are supplied by nature as a part of the animal mechanism. When once a hand is evolved capable of grasping artificial aids the invention of these devices has gone forward with leaps and bounds entirely unparalleled by the slow processes of the natural selection of bodily structures. Such a short cut to efficiency is an immense advantage as an evolutionary resource. Aside from man only the higher apes among animals make any attempt to use even such simple tools and weapons as a stone or a stick. The idea of fashioning anything to be held in the hand for any purpose whatsoever, is entirely human.

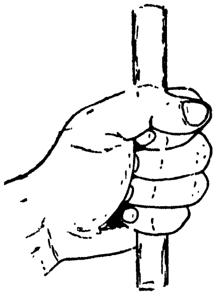


FIG. 164. — The opposable thumb.

Our absolute dependence upon an opposable thumb and a grasping hand may be emphasized if we imagine in detail an ordinary day's activities with two unusually sore thumbs. What laborer works without his hands? What artisan, even in the days of machinery, can produce anything without fingering it? The artist who creates a painting or statue must hold a brush or a chisel, and even the prize-fighter clenches his fist, with its tightly opposable thumb, in order to earn his daily bread. The mechanical performance of all writing and printing, with everything that this means in the communication of ideas, is primarily thumb and finger work, and the same is

true of most human activities that make up what we call civilization. The common phrase, "He had a hand in it," expresses exactly and literally the part dominant man has taken in the world's affairs.

5. Tactile Fingers

Not only is the human hand with its opposable thumb a structure which can effectively grasp a tool or a weapon but it is a delicate sense-organ as well which can, with great nicety, feel, hold and handle things. The balls of the fingers particularly are equipped with numerous sense-endings and the nails furnish protective shields for the finger-tips, while the arm-bones constitute a handle of extensible levers upon which this discriminative organ of contact is mounted.

The sense of touch is the great confirmatory sense underlying all sensory experiences with the external world. The baby, with its staring eyes, never really discovers its toes until it grasps them with its fingers, and so on throughout life the tactile fingers are continually learning, far more than is ever realized, about the character and geometry of the world with all that it contains. By handling over objects, putting them in different positions and placing them side by side or separating them from one another, the foundations of science are laid. Only upon such an underpinning of conscious or subconscious tactile sensation may the superstructure of reasoning, imagination and abstract thought be reared. Even a science as man-made as astronomy bases its incomprehensible distances upon tangible measurements near at hand. This is one of the reasons why animals not

possessing exploring hands are unable to enlarge their mental world beyond a certain limit.

6. The Evolution of Tools and Weapons

The very earliest traces of the existence of man on this earth are not his fossil bones but his handiwork. Fashioned flints, chipped or polished, are the first silent witnesses of the handy human hand, for man is a maker of tools and weapons as well as a user of them.

Let us consider briefly a half dozen kinds of primitive activities that serve for defence and maintenance wherein the hand of man has evolved instruments lifting him far above the plane of the beast.

a. Striking

It is said that an ape, when angered, will sometimes in frenzy tear a branch from a tree and brandish it menacingly. The movements of the ape in this instance are not well directed, however, and its grip is not very effective because of the shortness of the thumb.

Primitive man goes further, fashioning the cudgel into a war club. To-day even, man preserves a relic of the bludgeon of savagery when in ceremonial he bears aloft the mace of authority.

b. Throwing

Throwing is striking at a distance. Various things have been thrown by the hand of man all the way from the "smooth stone" of David's sling to the trench bomb of the modern grenadier.

When one has gone to the trouble of making a special

instrument to throw, it is deemed desirable sometimes to get it back again, and so the boomerang of the Australian came to be and the retrieving thong which was attached to the javelin or spear. From this javelin thong, perhaps, grew the idea of the bow-string with the bow that could throw the spear or arrow farther than the arm alone could. Then came the strong cross-bow with the bow mounted on a stock and with a trigger to regulate the shot, putting the bow and arrow in turn out of fashion. Guns and cannon, however powerful and elaborate, are simply throwing machines which have been developed to a frightful degree. It has been suggested that their forerunner is a blow tube such as the Malay natives still make of reeds to shoot their poisoned darts, only in one case the blowing of the missile is done by means of lung power and in the other by means of gunpowder.

c. Cutting

Sharp-edged flakes of flint or obsidian made the simple cutting tools of our ancestors of the ice age. It is easy to see how more power was gained by fastening the sharp flint by a thong to a handle, thus making a sort of an axe or adze out of it.

As soon as bronze and iron were conquered by man, lances and swords followed. The comparatively recent mastery of steel has made possible the evolution of a vast array of cutting tools of great efficiency.

By notching the edge of a sharp flint-flake a primitive saw was made and thus another pregnant idea in cutting instruments became a part of man's heritage.

d. *Boring*

No animal ever used a thorn or a pointed flint to make a hole in anything, but ancestral man did. Moreover, by boring a hole in one end of the boring tool itself, whether it was a thorn, flint splinter or slender bone, a needle was made and thereafter handiwork, ranging from the rude skin clothing of the caveman to the latest Paris creations, was made possible.

e. *Pounding*

The simplest tool for pounding is doubtless a stone that fits the hand. If one could not be found to fit, it could be battered and chipped until it did, and probably the earliest and crudest flint tools, the *eoliths*, were of this type. The next obvious thing to do was to fasten the pounding stone to a handle, and the father of all hammers appeared.

f. *Grinding*

Grinding is closely related to pounding and is one of the peaceful, rather than the warlike arts. First probably came a hollow stone and a rock held in the clenched fist, then mortar and pestle, and finally, millstones with machinery to turn them upon each other.

Thus all these various fundamental activities and others like them were at first *hand-work*. Even when the forces of nature, through the aid of machinery, were made to take over the tasks of man, it was the handy hand that fashioned the machine.

7. The Parts of a Human Foot

The human foot is made up of seven ankle-bones, five sole-, or instep-, bones, and five toes with a total of four-

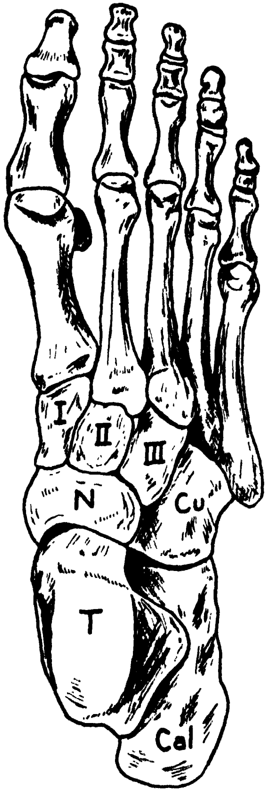


FIG. 165.—The right human foot as seen from above. *I, II, III*, first, second and third cuneiform; *Cu*, cuboid; *Cal*, calcaneus; *N*, naviculare; *T*, talus. (After Spalteholz.)

teen phalanges (Fig. 165). There are also two small sesamoid bones embedded in the tendon of the first metatarso-phalangeal joint on the under side, and sometimes other sesamoids at the remaining metatarso-phalangeal joints.

Traces of three rows of ankle-bones are present. In the first, or proximal row are the *calcaneus* and *talus*. The former is the largest bone of the entire foot and it extends backward to form the heel. Upon the latter, which is homologous to the scaphoid and lunate bones together of the proximal row in the wrist, the leg articulates. The middle row, the "centrale" bones of comparative anatomy, is represented in the *naviculare*. The third or distal row is composed of three *cuneiform* bones, each bearing a metatarsal, and the *cuboid* bone bearing two metatarsals.

The *metatarsals* themselves and the *phalanges* correspond to the homologous bones of the hand.

All the bones of the foot are bound together into a

weight-bearing unit by many ligaments, tendons and muscles, with the largest tendon of the entire body, the *tendon of Achilles* (Fig. 3), attached to the heel.

8. Contrast between the Foot and Hand

The difference between hand and foot in man is greater than in any other animal. In apes the functions of

FIG. 166. — The palm of the hand of an orang-outang, *Simia satyrus*, showing the poorly opposable thumb. (After Primrose.)

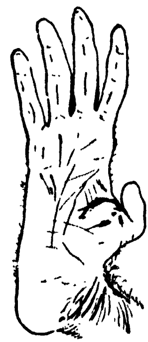


FIG. 167. — The sole of the foot of an orang-outang, *Simia satyrus*, showing the thumb-like big toe. (After Primrose.)

grasping and support are partly shared by both hand and foot (Figs. 166 and 167). In man, on the contrary, these two lines of activity have become entirely segregated, although some people can pinch with the big toe against the second, or flex all the toes enough to grasp awkwardly such an object as a handkerchief.

The ankle-bones, which must support the weight of

the body, form at least one-half of the entire foot while the wrist-bones do not make up more than one-sixth of the grasping hand with its long fingers. The longest

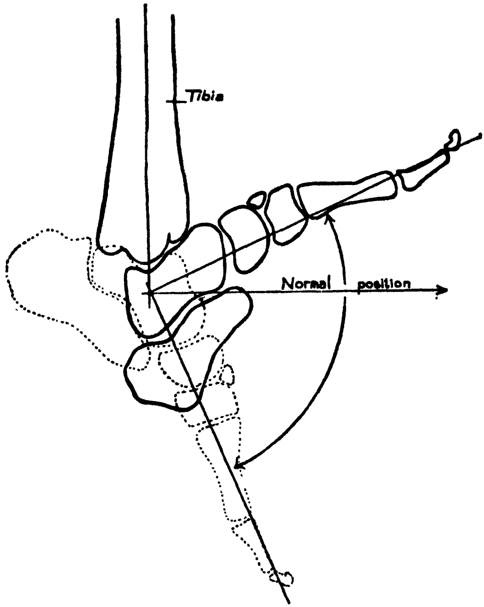


FIG. 168. — Diagram showing the normal extent of the hinge movement allowed by the ankle. Compare with Fig. 169.

toe is about one-fourth the length of the foot while the longest finger is full half the length of the hand.

The foot is arranged practically at right angles to the leg (Fig. 168) while the hand hangs straight down at the end of the arm, making an angle of 180° (Fig. 169). Moreover, bending at the wrist toward the palm side is easily accomplished through an arc of at least 90° while

the corresponding movement of the foot at the ankle is made with difficulty through a third of that distance, as shown diagramatically in Figures 168 and 169.

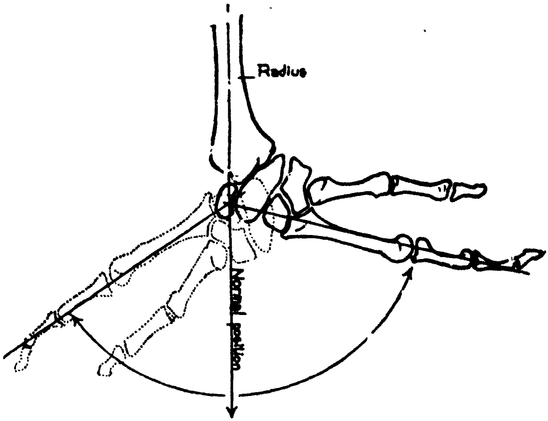


FIG. 169. — Diagram showing the normal extent of the hinge movement by the wrist. Compare with Fig. 168.

On the other hand, the swing away from the natural position in the opposite direction, which raises the foot up on the toes but accomplishes nothing useful for the grasping hand, is much freer and can extend through a larger arc in the case of the foot than it can in the case of the hand.

Rotation of the hand, which is gained through the way that radius and ulna are hung from the humerus, is present only in a slight degree in the foot. The tibia does not rotate on the fibula as the radius does on the ulna, so that the lateral swing of the big toe from right to left and back again is consequently limited. In hoofed animals, like the cow and horse, in which the

specialization of a supportive leg and foot has gone much further than it has in man, the rotary movement is en-

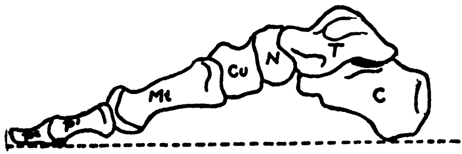


FIG. 170. — The long arch of the foot. *C*, calcaneus; *T*, talus; *N*, naviculare; *Cu*, cuneiform I; *Mt*, metatarsal; P^1, P^2, phalanges.

tirely lost. The prediction is that the soldier of the far distant future, if there is need of such an individual then, will have more difficulty than is experienced to-day in standing at attention with heels together and toes thrown out at an exaggerated angle.

9. The Arches of the Foot

The bones of the foot are arranged in the form of two arches, which act as springs or shock absorbers in locomotion. They also protect from pressure the nerves and blood-vessels of the sole.

FIG. 171. — A cross-section through the middle of the foot showing the transverse arch. (After Rauber.)

The *long arch* rests upon the ground both at the heel and upon the ball of the foot, or, in terms of the skeleton, upon the posterior end of the calcaneum and the distal ends of the metatarsals (Fig. 170). It has for a keystone the talus which bears the weight of the body and is the only bone of the foot that articulates with the leg.

The smaller *transverse arch* (Fig. 171) extends from

side to side through the distal ends of the metacarpals. In standing still the weight of the body rests principally upon the long arch. When the center of gravity of the body, however, is thrown forward as in walking, the weight of the body shifts temporarily to the transverse arch every time one comes up on the ball of the foot and the toes. Then when the weight is thrown forward, the transverse arch tends to flatten, allowing the toes to grip the ground so as to effectively push the body forward. This happens most perfectly in the case of the unrestrained bare foot that is not crowded into an unyielding hoof-like shoe. It is obvious that high-heeled shoes throw the standing weight forward so that the long arch does not function properly, and the transverse arch, which should be reserved for locomotion, gets more than its share of burden bearing.

Any arch resting on two pillars spreads its weight over a larger area making a more stable foundation than would be the case with a single column supporting the same amount of weight. The long arch of the foot is tipped up by a high-heeled shoe so that the line of gravity runs mostly through one pillar of the long arch instead of through two, consequently it no longer functions as an arch and all the mechanical advantages which an arch possesses are sacrificed. The awkwardness exhibited in walking on stilts or crutches is partly due to the absence of the double point of contact with the ground that is furnished by the arch. Again, tight shoes that do not allow the transverse arch to spread properly in walking, prevent the proper pull on the ground by the toes and add greatly to the mechanical difficulties of locomotion.

10. The Adaptation of the Human Foot

Human feet have never quite recovered from their surprise at finding the body tipped up on end and in having thrust upon them the entire responsibility of its support. They have done the best they could in the

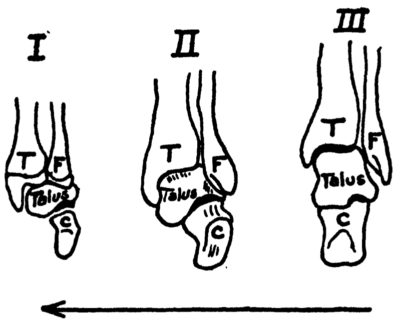


Fig. 172. — The heel as seen from behind of (*I*) a Chimpanzee, (*II*) an Australian, and (*III*) a Caucasian. The fibula (*F*) plays a decreasing rôle while the calcaneus (*C*) tends to shift in the direction of the arrow. (After Wiedersheim.)

evolutionary time they have had with the inherited materials that were on hand, but it must nevertheless be confessed that the result is as yet only a makeshift foot. The various foot troubles of man are an eloquent confirmation of this statement.

In the first place man needed to have a considerable part of the foot bent at right angles to the leg, so that it would come in contact with the ground and thus prevent the body from tipping over forward. At the same time a part of the foot, namely, the heel, had to be detailed to project in the other direction to prevent tipping

FIG. 173. — A footprint to show that the effective long arch is on the inner side of the foot.

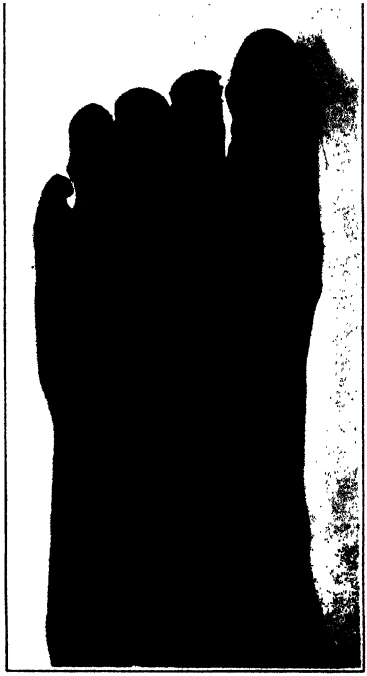


FIG. 174. — An Egyptian toe. The atrophy of the little toe in many modern feet is sometimes supposed to be due to wearing boots. But it seems to be a general evolutionary trend, which is tending to reduce the human foot to a single toe (the first or big toe). This foot of an Egyptian mummy of the XX dynasty, about 1300 B. C., shows that the little toe was in a deplorable state even then, centuries before boots appeared in Egypt. The last phalanx is diminutive and its joint is ankylosed. Photograph from Dr. Gorgy Sobhy, School of Anatomy, Cairo. (From the *Journal of Heredity*, 1917, page 541.)

backward. Thus the human foot became plantigrade as a mechanical consequence of bipedality. The swift horse, which perhaps has the most successful locomotor appendages of any quadruped, has no more need of plantigrade feet than the legs of a table which maintains perfect equilbrium without flat feet.

The flatness of the feet, however, has necessitated the formation of the arches mentioned in the last section and this has entailed adjustments in the case of every bone of the foot. That these adjustments are far from perfect is at once apparent when the arrangement of the bones of the foot is carefully scrutinized.

The ankle-bones, for instance, together resemble a cairn of irregular stones piled one upon another on the top of which is precariously balanced the weight of the body.

Furthermore, the big calcaneus bone is not squarely placed under the center of gravity as a foundation stone should be, but is rather to the outside of the line of weight. That it is gradually being shoved under, into a mechanically better position, is shown in Figure 172 where is pictured the less satisfactory adjustment in the case of the primitive Australian, as well as the condition in an ape.

This outside position of the calcaneus, like a run-over heel of a shoe, causes the weight of the body to veer over toward the inner, or big-toe side of the foot. The long arch, moreover, is considerably higher and more effective on the inner side of the foot than it is on the outside, as any print of a bare foot on the sand demonstrates (Fig. 173). The result is that the big toe is becom-

ing larger while the little-toe side of the foot is degenerating. An examination of Egyptian mummies shows (Fig. 174) that the degeneration of the little toe antedates by far the wearing of tight shoes, which have so frequently been blamed for the demoralization of the little toe, since it was already manifest among these ancient sandal-wearing people.

The big toe is said to be relatively somewhat longer in the male than in the female, which, if true, would be evidence that the male, with his feet if not with his head, has travelled a little farther on the evolutionary highway than has the female of the species.

In general it may be concluded from the comparative anatomy and embryology of the human foot that it is a makeshift organ of support, adaptively constructed out of a grasping apparatus by the rearrangement and enlargement of the tarsal bones, the shortening and compacting together of the metatarsals and phalanges, and the introduction of the arches.

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All numbers refer to pages. Genera are given in italics: names of men in small caps. Blackface numbers refer to figures.

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